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A Half Century of Natural Transitions In Mixed Hardwood Forests

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SUMMARY

One of the more enduring features of our landscape is forest. By land or by air the conclusion is the same: the forest is everywhere. But it wasn't always so. The history of the Connecticut forest is simply summarized: elimination, exploitation, recovery.

The subject of this Bulletin is the recovering forest. The natural changes occurring in 50 years on 10 acres of sample representing nearly 200 acres on four hardwood forests in central Connecticut are tabulated for 1927, 1937, 1957, 1967, and 1977. Similar tabulations are made for a sample of 1.6 acres burned in 1932. The source of the tabulations are the records of nearly 35,000 stems present during all or part of the 50 years.

In 1927, 37 species were tallied; 50 years later 34 were still present. Although numbers declined from 1500 stems per acre in 1927 to less than 800 in 1977, diversity decreased only slightly. Basal area increased from 70 ft^2 per acre in 1927 to 99 in 1977. The steady increase was interrupted by a 7 percent loss during 1957-67, a decade with drought and defoliation. Despite defoliation, during the succeeding decade the increase resumed and basal area returned to its former level. Surprisingly, increase in basal area during 50 years was greatest on the dry sites where mortality was low.

About 63 percent of all stems were single, presumably grown from seedlings; the remainder were sprouts. Despite 50 years of mortality and ingrowth the percentage of sprouts in the entire stand remained nearly constant. In the canopy, however, single stems persisted more than sprouts.

In 1932 fire swept across part of one tract, killing all minor species and saplings of major species but leaving the larger stems intact. After 25 years the burned tract had the numerous stems typical of a young forest but the basal area of a more mature forest. By 1977 the burned forest was recovered with basal area and number of stems slightly more and with little change in composition compared to the unburned portion. Fire interrupted the natural change and set it back about three decades.

By dividing the sample into fortieth-acre plots and noting changes during each period of observation sets of transition probabilities were estimated describing species predominant in number or basal area or the changes among diversity or tolerance. For example, of the plots where maple was most numerous in 1927, 82 percent remained in 1937, 7 percent became dominated by oak, 4 by birch, none by other major species and on 7 percent minor species became most numerous. Similarly, of plots designated maple in 1967, 67 percent remained maple and 0, 21, 4 and 8 percent became designated oak, birch, other major and minor species. Despite the passage of 40 years the transitions remained similar. Steady states extrapolated from these transitions differ slightly in detail but depict a future forest rich in maple, birch and minor species but poor in oak and other major species. When basal area was used as the criterion for classification the same trends were observed; a forest becoming richer in maple and birch, poor in minor species and reduced in oak but not to the obscurity predicted by transitions for number of stems. When tolerance to shade rather than species groups was examined a surprising number of plots were dominated by moderately tolerant species: During 50 years the proportion of the forest dominated by tolerant or very tolerant grew. The forest predicted at steady state, however, was not markedly different from its present state: 60 percent occupied by moderately tolerant, 18 percent each for tolerant and very tolerant and less than 2 percent for intolerant.

Front Cover: A central Connecticut field and woodland as it looked in 1920. How this unmanaged area had changed after four decades is shown on the back cover.

A HALF CENTURY OF NATURAL TRANSITIONS IN MIXED HARDWOOD FORESTS

George R. Stephens and Paul E. Waggoner

For about a half century, while we ate food from elsewhere and burned fuel from elsewhere, our Connecticut land has been reverting to forest. Thousands of our three million acres are still farmed for food, and we have built upon or paved over thousands more. Nevertheless, after three centuries of cutting, grazing and plowing and decades of fire and blight, much of our land has been quietly growing a new forest. Now, seemingly suddenly, the mass of wood slowly accumulated in our new forest multiplied by a new demand for nearby fuel and lumber interests us.

How did this newly valuable forest grow while most of us were thinking of The Charleston, Depression and World War II and then the Cold War, Viet Nam and inflation? What is the forest now made of? And how may it change?

Now that the forest is valuable it is too late to observe how it grew. Fortunately, however, 52 years ago five men from this Station set out to Central Connecticut to study what was then scarcely a forest (Hicock et al., 1931). The four tracts they examined included land that had never been tilled and land that had. The front cover shows a tract that they saw. They examined transects of land a rod wide. Although we would now say the transects are 5 meters wide, we would still say the transects go up hill and down, through muck among poison sumac, over deep soil among red maple, and then onto stony land among black birch. Later, fire swept over part of one of the tracts. Still later insects defoliated parts of the tracts. Thus the land they encompassed represents much other land in the Northeastern United States.

Not much escaped these five pioneers. They identified, measured and mapped every stem larger than a half inch. A decade later, in 1937, they repeated their examination, in 1957 and 1967 other men from the Station repeated the examination, and now after a half century and observations in 1977, we can report how our newly valuable forest grew.

We can, of course, report what these representative Connecticut forests are made of, the species, their numbers and size. These characteristics, which one can call ecological, are reported here. The characteristics of the forest that pertain to timber will be reported later in another Bulletin.

Finally, from the transitions of the past half century, we can predict how these representative forests will change in the years to come.

As the decadal surveys were made they were reported: the 1927 survey by Hicock et al. (1931), the 1937 and 1957 surveys by Collins (1962) and Olson (1965), and the 1967 survey by Stephens and Waggoner (1970). For the convenience of the reader of our present Bulletin and because some of the earlier reports are out of print, we shall repeat much data from the earlier surveys and add the 1977 observations.

DESCRIPTIONS OF THE TRACTS, WEATHER AND PESTS

We know that our seemingly new forest is of two types: i) continuously forested and ii) risen during the last 150 years. Of the first, most was cut or ravaged by fire, but it was never completely cleared for agricultural pursuits. Some of this forest is likely little different in general appearance and composition today than when the colonists first landed on our rocky soil. We can see this forest on our gaunt ridges, too steep and stony to plow, too rocky to support cattle or sheep. Nonetheless repeated cutting, fire, and the sudden loss of chestnut have altered the composition of this remaining original forest.

The forest risen during the last 150 years has grown on land once pastured or plowed. Here the changes are spectacular, clearly visible, and quickly accomplished during a man's life span. The unmown meadow and fallow field are quickly invaded by small-statured shrubs and short-lived pioneers such as sumac and sweetfern, redcedar and birch. The idle furrow is host to the light-seeded birch and aspen, while birds scatter the heavier seed of redcedar and shrubby dogwoods. Often quick to follow are cherry and sassafras, and sometimes pine. Sparsely at first, and then more and more, these pioneers rise up from unmown meadow and forgotten field. As 15 or 20 years quickly pass, the shrub-dotted fields are transformed to a tangled thicket that blocks the vista of rolling fields and stone walls. Forest, of a sort, now claims the land.

Soon the more majestic, long-term invaders appear. Oak and hickory, maple and ash emerge from the thicket to claim the old field. The lowly pioneers falter and dwindle, unable to remain in the race for the sun. The forest now assumes more of its permanent character, and the insidious struggle of size and numbers, unnoticed by all but the most persistent observer, replaces the dramatic change from field to forest. Our Bulletin describes this insidious natural struggle in four mixed hardwood forests of central Connecticut.

This study began in 1926 on an 80-acre tract called Turkey Hill in the Cockaponsett State Forest in south central Connecticut. In 1927 study began of the 50-acre Cox tract, the 40-acre Reeves tract, and the 40-acre Cabin tract, all in the Mountain Block of the Meshomasic State Forest in central Connecticut. These were selected as representatives of forests and sites in the mixed hardwood region that covers most of Connecticut and large areas of New York, New Jersey and Pennsylvania.

All tracts are near the western end of the Eastern Highlands of Connecticut, a region of metamorphic rocks and glaciated soils. The topography is gently rolling to rugged with considerable rock outcrop. Elevation ranges from 400 to 800 feet. Of the four tracts, Turkey Hill is most exposed to strong southeasterly gales such as those that occurred during the 1938 hurricane.

The forest cover was the mixed hardwood type typical of much of the woodlands in Connecticut, with 37 species represented on the transects. In 1927 the trees varied from 25 to 40 years in age with occasional older trees. To a forester's eye portions of the forest on Cox seemed the most newly risen and that on Cabin the oldest. The forest on Turkey Hill seemed younger than that on Reeves. Observation and inquiry revealed that portions of each tract had been cleared in the past, but the exact boundaries of clearings could not be ascertained. Thus both the forest that has never been tilled and the forest that has arisen on old fields are represented in the tracts but could not be clearly separated. Chestnut was present on all tracts as evidenced by continued sprouting. Since the study was started in 1926 and 1927, disturbance by man has been slight, and the disturbed areas have been eliminated from this study; a burned area on Turkey Hill is analyzed in a separate Chapter.

The normal precipitation is 44 inches

per year at Hartford's Brainerd Field, which is about 10 miles north of three of the plots. In the first decade of the census of the tracts, the annual precipitation was 3.6 inches less than normal. In the score of years between 1937 and 1957, it was 1.0 inches above normal. Drought occurred during 1958-67, and precipitation was 6.9 inches below normal. During 1968-77 it was 2.2 inches above normal. Thus a decade of dry, a double decade of normal, a decade of very dry, and a decade of moist weather occurred in the half century.

In the middle years of the decade 1957-67 gypsy moth (Lymantria dispar L.), cankerworm (Paleacrita vernata Peck.) and other defoliators flourished and attacked the leaf canopies of all four tracts. Defoliators varied with tract and year, but more important to the forest was the degree of defoliation. Aerial reconnaisance indicated partial defoliation on Cabin, Cox and Reeves during 1961, 1962 and 1963 and on Turkey Hill in 1964. In 1962 on Cabin, Cox and Reeves removal of the leaf canopy was estimated to be greater than 50 percent. In 1963 Cabin and Cox were less than 50 percent defoliated, while portions of Reeves may have been more than 50 percent defoliated. In 1964 removal of the canopy on Turkey Hill was estimated to be between 25 and 75 percent.

The middle years of the decade 1967-77 were also a time of defoliation by the gypsy moth and the elm spanworm (Ennomos subsignarius Hbn.). In 1971 Cox was defoliated more than 75 percent. Canopy removed on Cabin and Reeves was estimated between 25 and 50 percent, while on Turkey Hill defoliation was only 10 to 25 percent. No further defoliation was recorded for the decade.

The maps of defoliation are in the files of the State Entomologist, New Haven.

The significant diseases in the forests were chestnut blight and Dutch elm disease. By 1927 blight had killed the large chestnuts, and during the next 50 years it kept on killing chestnut sprouts that grew from old roots. Dutch elm disease reached the plots during 1937-1957.

METHODS

All tracts were laid out as rectangles with the long axis east-west. The dimensions were: Turkey Hill, 20 x 40 chains; Cox, 14 x 36 chains; Reeves, 10 x 40 chains; and Cabin, 20 x 20 chains. A chain is 66 feet or 20 meters and an acre is 10 square chains. Transect lines were north-south at 5-chain intervals on Turkey Hill and at 4-chain intervals on the other tracts. Characteristics of site such as soil type, soil depth, soil drainage or moisture, stoniness, humus type, slope, and aspect were determined and mapped along the transect lines. Along a strip 0.25-chain wide centered on the transect lines, each tree 0.6 inch d.b.h. or greater was plotted on a map, identified, and described. D.b.h. is diameter breast high or 4.5 feet above the ground.

Initially, description included d.b.h., crown class (on all tracts except Turkey Hill), and whether or not the tree was a member of a sprout group. Witchhazel was not recorded on Turkey Hill in 1926, but it was beginning in 1937. Crown class is defined in Forest Terminology (Soc. Amer. Foresters, 1950).

In 1937 the same information was recorded for stems tallied in 1927. Deaths and new trees (ingrowth) 0.6 inch d.b.h. or larger were noted. Crown class was recorded on Turkey Hill in 1937.

In 1957 the same information was again recorded, but the minimum d.b.h. was decreased to 0.5 inch. In addition, the height of all dominant trees and every tenth tree other than dominants was measured with an Abney level. Trees for which height was measured and any companion sprout were also examined for defects. The defects were in form and symmetry and those caused by injury to the stem or crown and do not include internal defects such as heartrot.

In 1967 all trees larger than 0.5 inch d.b.h. were measured at d.b.h. Also they were classified for crown class, and new sprout numbers were assigned where

death had carried one away or a new one had appeared.

In 1967 some trees that had recently died and were still standing were included in the populations counted. In the tables that we now publish these are counted as dead in 1967, their deaths are counted in 1957-67, and these populations of 1967 in our present tables are slightly changed from earlier ones (Stephens and Waggoner, 1970).

In 1977, the tracts were examined as in 1967.

In 1932 a resurvey of the Turkey Hill tract was made following a fire that burned over approximately 40 percent of the area. In addition to the same information gathered in 1926, the extent of the fire on the transect lines, deaths, new recruits, and crown class were recorded. Trees alive in 1926 but dead in 1932 were arbitrarily assigned to the lowest crown class. The information from the burned part of Turkey Hill appears in a separate Chapter in this Bulletin.

The vigilance of the State Foresters has protected the sites from other disturbance remarkably well. Eighty-five percent of the original 13.75 acres encompassed in the transects was undisturbed a half-century later. The areas disturbed at any time were omitted from our analysis, which uses the areas shown in Table 1. Since nearly 35,000 stems were observed during the half century, their records were analyzed by machine.

Table 1. Sample area (acres) of moisture classes, undisturbed sites only.

	Muck	Moist	Medium Moist	Dry	All
Turkey Hill	0.16	0.57	1.57	0.09	2.40
Cox	0	0.51	2.05	0.60	3.16
Reeves	0	0.32	1.38	0.70	2.40
Cabin	0	0.33	1.82	0	2.15
All	0.16	1.74	6.83	1.39	10.12
Burned	0	0.20	1.09	0.30	1.59

The nature of the forest and its changes can be expressed in several ways: the appearance and disappearance of species, the rise and fall in population, and the change in size and dominance. Sprouts, defects and the effects of fire, drought and defoliation can be observed. The statistical methods that we used to make all this comprehensible are described in the separate Chapters.

SITE CHARACTERISTICS

The four tracts represent forests of the region and comprise a mosaic of previous land use. The boundaries of different use and, hence, ages of the forest could not be precisely determined (Hicock et al., 1931). The presence of certain indicator species, however, tells us that a tract, or some portion, recently reverted to forest from open field. Their absence generally indicates that forest has covered the land at least several decades. The presence in 1927 of redcedar, gray birch and bluebeech, all pioneers, indicated that the forest on Cox is the youngest. Because Cabin had few pioneers, it was likely forested for a long time. Turkey Hill, burned and unburned, and Reeves had fewer pioneers than Cox, but their presence suggests that portions of these tracts had recently reverted from open field.

Although soil type, depth of soil, internal soil drainage, stoniness, humus type, and aspects were determined along the transects (Hicock et al., 1931), only internal soil drainage is used here in relating tree or stand characteristics to site because past studies indicated it to be the most important one.

Soil drainage classes were classified according to the Soil Survey Manual (Anonymous, 1951). In addition to the seven classes given in the Manual, one was added for the muck site on Turkey Hill. Because the area sampled in some drainage classes was small, the classes 0-7 were combined into four moisture classes as follows: (A) muck, 7; (B) moist sites which included 0, the very poorly drained, and 1, the poorly drained; (C) medium moist sites which included 2, the imperfectly or somewhat poorly drained (only .06 acre), 3, the moderately well drained, and 4, the well drained; and (D) dry sites which included 5, the somewhat

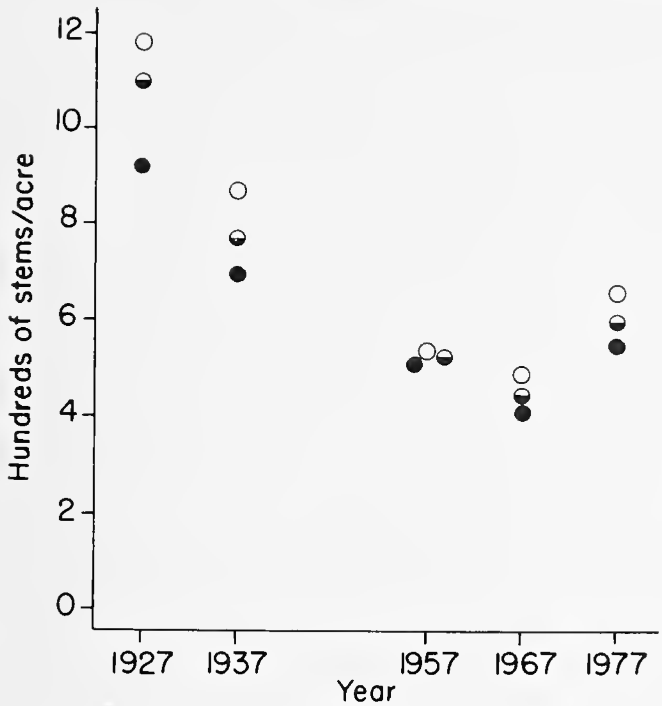

Fig. 1. The number of major species stems per acre on moist (●), medium (◒) and dry (○) sites.

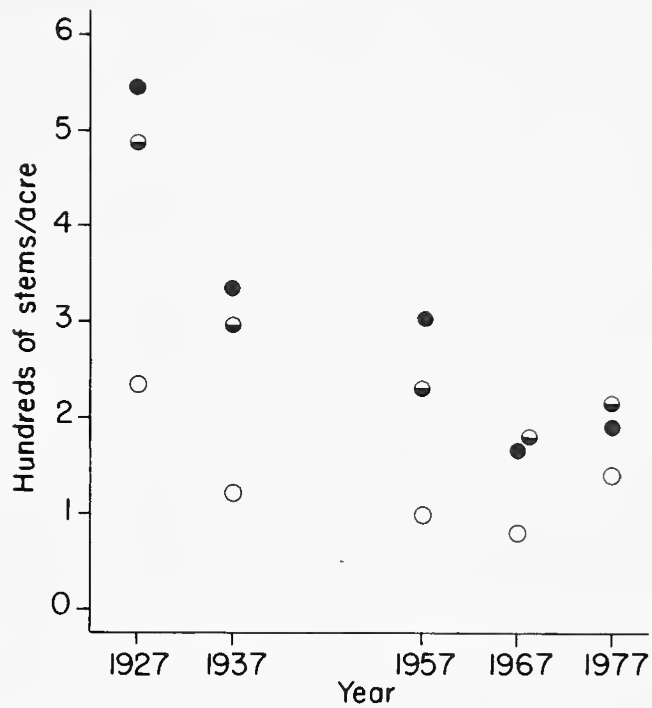

Fig. 2. The number of minor species stems per acre on moist (●), medium (◒) and dry (○) sites.

excessively drained, and 6, the excessively drained soils. The area in each combined moisture class is shown in Table 1.

The abundance of pioneer species on certain moisture classes leads us to conclude, for example, that much of the moist and medium moist site on Cox represents new forest. Similarly, the medium moist site on Turkey Hill and the dry on Reeves also contain relatively young forest.

NUMBER OF STEMS

From 1927 to 1967 the number of stems declined steadily and then increased from 1967 to 1977. For "number of stems" we shall write "numbers". On sites of all moistures the numbers of major species declined from about a thousand per acre to about 500 (Fig. 1). The numbers of minor species declined from about 500 to less than 200 on moist and medium sites, whereas on the dry sites their numbers were always low, falling from about 250 in 1927 to less than 100 in 1967, and suggesting that the dry sites had small ability to support an understory of minor species (Fig. 2).

Following the defoliation during the 1960's and 1970's, the numbers of both major and minor species increased, showing the advantage to new stems of both the temporary removal of the overstory by insects and the permanent removal of large trees by death (Fig. 1 and 2).

Comparing the four tracts in Fig. 3 and 4, one sees at once the many stems in 1927, particularly of the minor species, on the youngest tract, Cox; by 1957 this large number fell to nearly the level on the other three tracts. On the tract that had probably been grazed shortly before 1927, Turkey Hill, the numbers in 1927 were low, and unlike the other tracts, Turkey Hill did not experience an increase in numbers from 1967 to 1977. Over all the tracts, moisture of soil had no average effect because stems of major species were the most numerous on moist in the Cox tract, on medium moist in Turkey Hill, and on dry in Reeves. These are the same tracts and sites believed to have recently reverted to forest.

Now, what were the species of the stems? Over all tracts and moisture

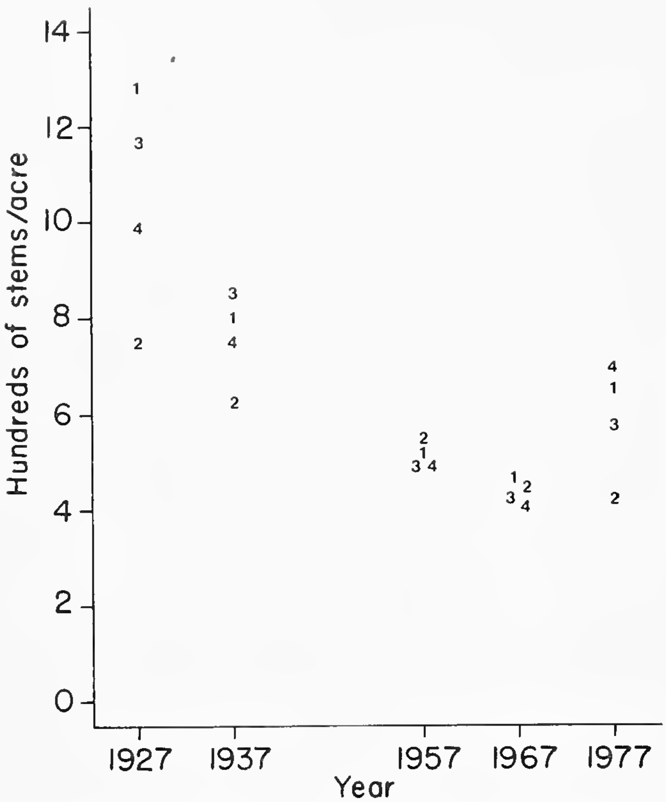

Fig. 3. The number of major species stems per acre on Cox (1), Turkey Hill (2), Reeves (3), and Cabin (4) tracts. The numerals indicate the relative age of the forests, with Cox (1) being the youngest.

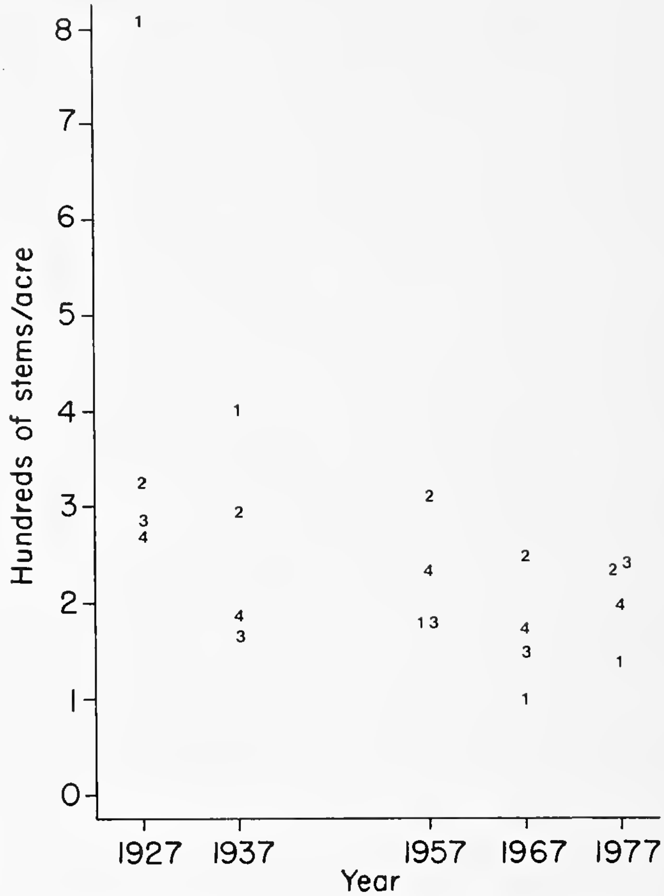

Fig. 4. The number of minor species stems per acre on Cox (1), Turkey Hill (2), Reeves (3), and Cabin (4) tracts.

classes in a single year, the answer is fairly easy. Since we have already dealt with total numbers and are now concerned with distribution of those numbers among species, we shall deal with percentages (Table 2). In 1927 red maple contributed fully a quarter, black plus yellow birch a fifth, and red plus white oak another fifth of the stems. No other species contributed a tenth. By 1977, red maple had increased to a third, the two birches to a third and red and white oak had declined to a twentieth. Only beech had come from insignificance to approach a tenth (it was 7 percent). This comparison of species over all moisture classes is comprehensible.

When we compare the species from site to site or tract to tract and from time to time, the 37 species, however, are bewildering. As a guide to the interesting interactions of place with species we calculated the deviation of a percentage in a time and place from the percentage expected if place had no effect. A hypothetical example illustrates. On two sites at two times 100 trees are distributed among Red, White and Other species as follows:

	Site A		Site B	
	Time 1	Time 2	Time 1	Time 2
Red	20		40	
		20		60
White	40		20	
		60		20
Other	40		40	
		20		20

At time 1 the average, or expected, value over sites A and B is for Red, 30, and for White, 30. At time 2 the expectation

Table 2. Number of stems of major and minor species (percent of total major or minor), all tracts. The letter i indicates 0.1 to 0.9 percent and Q indicates the species is present but less than 0.1 percent. Sum over all moisture classes includes trees on muck.

Major Species	Moist					Medium Moist					Dry					All				
	1927	1937	1957	1967	1977	1927	1937	1957	1967	1977	1927	1937	1957	1967	1977	1927	1937	1957	1967	1977
Sugar maple	8	11	15	16	12	3	4	6	7	6	1	1	2	2	2	4	5	7	8	6
Red maple	29	29	26	27	20	24	25	28	32	33	25	24	30	37	39	25	26	28	33	32
Red oak	8	8	8	5	3	10	10	9	6	4	8	8	8	6	4	9	9	9	6	4
Black oak	1	i	i	i	i	3	3	3	2	1	8	9	7	5	3	3	4	3	2	2
Scarlet oak	1	1	i	i	i	2	2	2	2	1	4	4	4	3	2	2	2	2	2	1
White oak	4	3	2	i	i	13	11	5	2	1	16	17	9	3	2	12	10	5	2	1
Chestnut oak	2	3	2	i	i	3	4	5	2	2	2	2	2	2	2	3	3	4	2	1
Yellow birch	17	20	22	24	29	8	9	12	13	18	i	i	1	1	2	8	9	12	13	17
Black birch	5	5	7	9	12	12	14	15	19	19	14	16	22	27	30	12	13	14	18	20
Paper birch	0	0	0	0	0	i	i	i	i	Q	0	0	0	0	0	i	i	i	i	Q
Bitternut hickory	i	i	0	0	i	i	i	i	Q	Q	0	0	0	0	0	i	i	i	Q	Q
Mockernut hickory	i	i	i	i	i	1	1	1	1	i	2	2	2	1	i	1	1	1	i	i
Pignut hickory	1	1	1	i	i	4	3	2	1	i	8	8	4	2	i	4	3	2	1	i
Shagbark hickory	i	i	1	1	i	1	1	1	i	i	i	i	i	i	i	i	i	1	i	i
Beech	i	i	3	5	6	1	2	3	5	7	2	3	5	7	9	1	2	3	5	7
Tulip	1	1	1	1	4	1	1	1	1	2	i	i	i	i	i	1	1	1	1	2
White ash	7	6	6	5	3	7	6	4	3	1	2	2	1	i	0	6	5	4	3	1
Black ash	i	i	i	i	i	Q	Q	0	0	0	0	0	0	i	0	i	i	i	i	i
Basswood	i	i	i	0	0	i	i	Q	Q	Q	0	0	0	0	0	i	i	i	Q	Q
Elm	2	2	2	i	i	i	i	Q	Q	Q	Q	0	0	0	0	i	i	i	i	i
Bigtooth aspen	4	3	0	0	0	i	i	i	Q	0	2	i	0	0	0	1	1	i	Q	0
Quaking aspen	Q	Q	0	0	0	0	0	0	0	0	0	0	0	0	0	Q	Q	0	0	0
Pepperidge	2	2	2	3	6	i	i	i	i	i	i	i	i	i	i	i	i	i	1	1
Locust	0	0	0	0	0	0	0	0	0	0	i	Q	i	i	i	Q	Q	Q	Q	Q
Butternut	i	Q	0	0	0	i	i	0	0	Q	i	i	0	0	0	i	i	0	0	Q
Black cherry	3	i	i	0	0	i	i	0	0	Q	i	i	0	0	0	1	i	Q	0	Q
Sassafras	1	i	2	2	2	1	i	1	2	4	2	i	1	3	4	1	i	1	2	4
White pine	0	Q	0	0	0	Q	Q	i	0	Q	0	0	0	0	0	Q	Q	i	0	i
Hemlock	Q	Q	i	i	i	Q	Q	Q	Q	Q	0	0	0	0	i	Q	Q	i	i	i
Redcedar	0	0	0	0	0	i	Q	Q	0	0	i	0	0	0	0	i	Q	Q	0	0
Stems/acre	919	692	502	411	546	1100	766	513	439	590	1179	866	532	482	652	1067	759	512	440	587
Minor Species																				
Chestnut	i	i	4	5	8	2	i	18	26	24	11	3	44	60	65	2	i	16	24	25
Dogwood	3	3	5	12	13	10	15	16	22	25	9	13	.9	12	7	9	12	13	19	21
Shadbush	5	6	1	i	1	3	4	i	i	i	10	11	3	4	1	4	5	1	i	i
Hophornbeam	6	6	9	1	i	8	7	5	1	1	7	12	13	i	2	8	7	7	1	1
Gray birch	16	10	i	0	0	14	9	i	Q	0	28	24	0	0	i	16	10	i	i	Q
Witchhazel[1]	20	29	51	59	65	20	29	37	42	45	13	14	17	22	23	20	28	39	43	46
Bluebeech	50	46	30	22	12	42	35	22	9	5	21	24	14	2	2	42	37	23	11	6
Stems/acre	543	333	302	170	191	486	296	230	178	215	235	122	99	80	140	454	274	222	161	198

[1] Witchhazel was not counted on Turkey Hill in 1927.

becomes 40 for both Red and White.

The interesting interactions of site with species at time 1 are the deviations from the mean or expectation for the species and time: Red was 10 poor and White was 10 rich on Site A. One could say the deviation or impoverishment in Red was 1/3 of the expected 30 or 1/10 of the total population of trees on the site at that time. The first is a species' point of view, the second is the forest's point of view, and we took the forest's view. At time 2 the effects or interactions were greater: Red had become 20 or 1/5 poor and White had become 1/5 rich on site A. So much for interactions of site with species at a time.

The interesting interactions of time with species at a site can also be seen as deviations from the mean for the species and site. For two times, however, it is more straightforward to compare the changes, species by species and site by site. In the hypothetical example above, the outstanding or differential increases are White on site A and Red on site B. Now some real results.

On the moist sites in 1927 the forest was relatively rich in yellow birch and sugar maple and poor in black birch and white oak; and in 50 years it became even richer in yellow birch and sugar maple, and poor in black birch, and surprisingly, in red maple. Remember, rich and poor are relative to the percentages of the species at a given time over all sites.

On the medium moist sites in 1927 the forest was average and remained so.

On the dry sites in 1927 the forest was relatively rich in white and black oak and poor in yellow birch. In 1977 it was rich in black birch and red maple and poor in sugar maple and -- still and especially -- poor in yellow birch.

The outstanding differential changes among moisture classes during the half century were:

Red maple lost on moist and gained on other sites.

White oak lost, especially on dry sites.

Yellow birch gained, especially on moist and medium, while black birch gained, especially on dry sites.

Pignut hickory lost, especially on dry sites.

White ash lost on medium moist sites.

Pepperidge gained on moist sites, and bigtooth aspen lost.

Among the minor species, chestnut, flowering dogwood and witchhazel all increased in numbers and proportion, while bluebeech and hophornbeam declined.

Among the tracts, species differed. Deviations were examined for six species in 1927 and 1977: red and sugar maple, red and chestnut oak, yellow and black birch. There were no peculiarities of the changes in species over the half century that were consistently related to the age of the forests on the tracts.

Muck was present only on the Turkey Hill tract, and the species found there are shown in Table 3. Yellow and black birch increased on muck as on the other three moisture classes, but beech was not present on muck. The number of red maples and white ash increased until 1957 and then declined, but their proportions merely fluctuated over the years. Black ash increased until 1967 and then declined. The big loser was American elm, which was removed by disease. Pepperidge disappeared from muck although it increased on moist sites. Turning to minor species, one sees that on muck witchhazel increased, while shadbush disappeared, and bluebeech decreased markedly during the fifty years.

DIVERSITY

In addition to the sheer change in numbers of stems and a few anecdotes about interesting species, the reader will want to know how big the stems are and how diverse is the collection of species. We will postpone stem size to later sections and discuss species diversity here.

Diversity in any forest is usually assumed to be a virtue. Certainly the pleasure of walking through the woods increases with the number of kinds of plants that the walker discovers. The pleasure from a forest landscape increases if leaves of different tints

Table 3. On muck, the number of stems of major and minor species (percent of total major or minor). The letter i indicates 0.1 to 0.9 percent and 0 indicates the species is present but less than 0.1 percent.

Major Species	1927	1937	1957	1967	1977
Sugar maple	0	0	0	1	0
Red maple	70	76	64	61	72
Red oak	0	0	1	1	2
Yellow birch	2	2	6	4	6
Black birch	0	0	1	3	2
White ash	10	13	17	16	11
Black ash	2	2	3	6	6
American elm	12	7	7	7	2
Pepperidge	4	0	0	0	0
Stems/acre	308	283	431	431	326
Minor Species					
Shadbush	25	25	8	11	0
Witchhazel[1]	0	25	50	56	83
Bluebeech	75	50	42	33	17
Stems/acre	25	25	74	55	37

[1] Witchhazel was not counted on Turkey Hill in 1927.

expand at different times, if various flowers appear in various seasons, and if a spectrum of autumn colors is seen -- all because of the diversity of the species. Finally, diversity is assumed to be a sort of insurance because a single pest will not likely attack diverse species.

Since diversity has several facets, however, measuring it is not simple (Pielou, 1966). In a finite forest, such as the transects through the Connecticut forests, the diversity decreases whenever an individual is lost, a species is lost or individuals become concentrated in fewer species. This composite character, diversity, can be measured as

$$\frac{1}{N} \log_2 \frac{N!}{N_1!\, N_2! \ldots N_s!} \quad \text{bits/individual}$$

N is the total number of individuals on the tract and N1, N2..., Ns are the numbers in the first, second, ..., and last of s species.

The behavior of this index with changes in the factors (numbers, species, and distribution) has been described fully by Pielou. Here we shall go directly to the changes over the decades in the factors and summarize by examining the change in the index of diversity.

Certainly the number of stems has decreased, Table 2. When the number of stems is large, however, as it is in our tracts even in 1967, both our common sense and Pielou's mathematics say declining numbers will have little effect upon diversity.

The number of species counted on the tracts has remained fairly constant. The table for 1927 shows 37 species, and the table for 1977 still shows 34 species. Only bigtooth and quaking aspen and redcedar disappeared, and these three species had contributed few stems in 1927.

Since there are no great changes in the relative contributions of the species as seen in the percentages of Table 2, and since the population has not declined to a sparse one, one expects that the index of diversity will not have changed greatly. In fact, it was 4.16 in 1927, 4.05 in 1937, 4.00 in 1957, 3.76 in 1967 and 3.59 in 1977. The diversity was much less on muck and showed no trend. It was slightly greater on medium moist than on moist or dry, but the slow decrease was evident on all these three moisture classes.

One might have expected that diversity would have increased with the development of the forest toward maturity, but this did not happen. Nevertheless, the inhabitant of the suburban forest may be reassured that he can see nearly as much diversity in trees when he hikes through the woods as his father saw when he looked for a lost cow.

BASAL AREA

Both stocking and maturity of a stand are revealed, but not by the number of stems or diversity of species, but by the cross-sectional area of the stems per acre. The cross-section is measured at breast height and called "basal area."

The basal area of major species, as an average over all tracts and sites, increased from 63 ft^2 per acre in 1927 to 97 ft^2 in 1957 (Fig. 5).

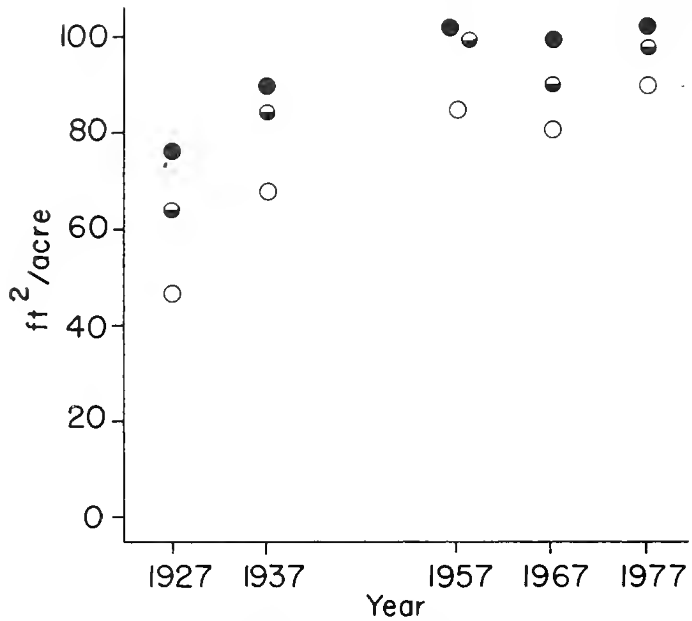

Fig. 5. The basal area of major species (ft^2/acre) on moist (●), medium (◒) and dry (○) sites.

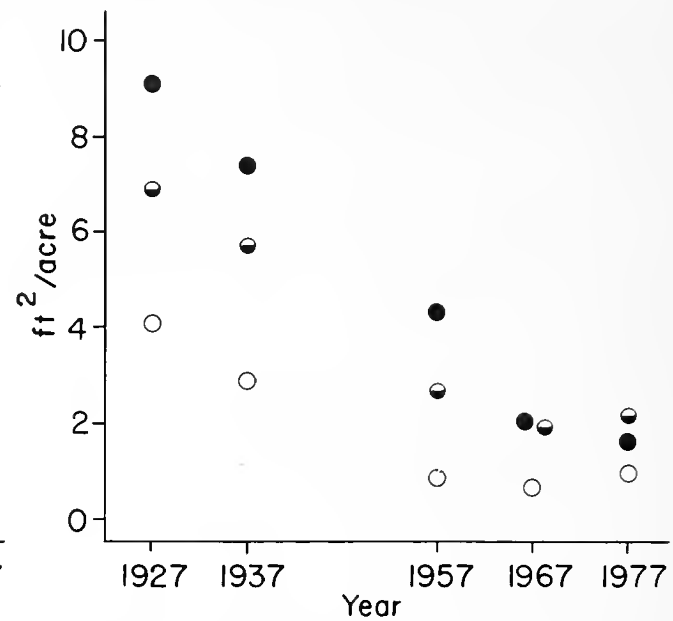

Fig. 6. The basal area of minor species (ft^2/acre) on moist (●), medium (◒) and dry (○) sites.

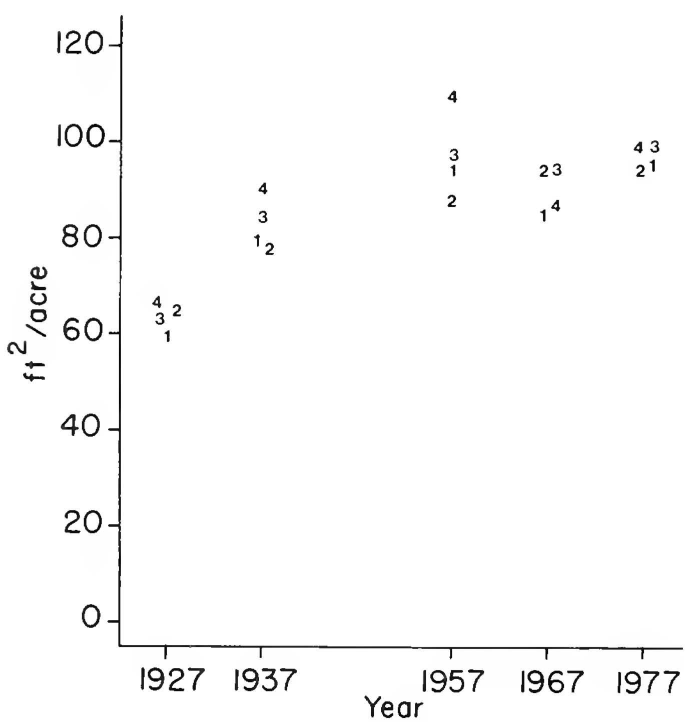

Fig. 7. The basal area (ft^2/acre) of major species on Cox (1), Turkey Hill (2), Reeves (3), and Cabin (4) tracts.

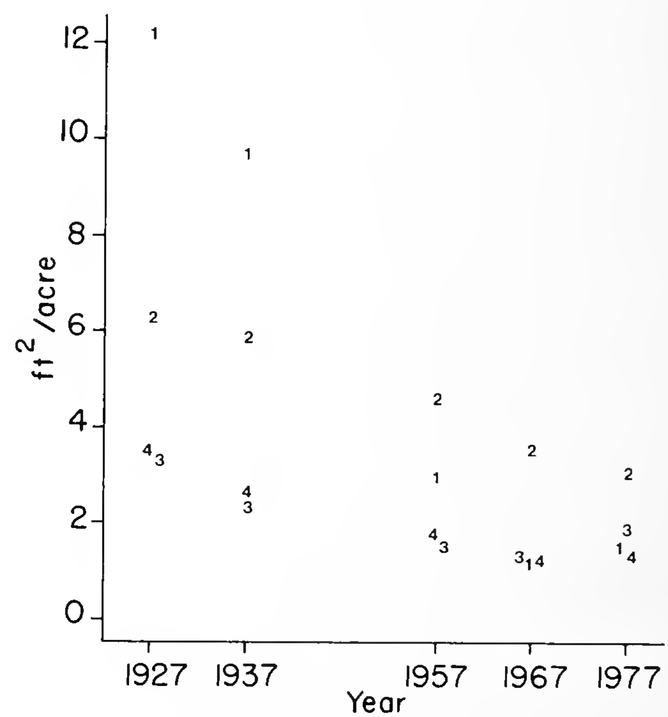

Fig. 8. The basal area (ft^2/acre) of minor species on Cox (1), Turkey Hill (2), Reeves (3), and Cabin (4) tracts.

Then basal area decreased to 90 in 1967 and recovered to 97 in 1977. Although basal area was always greatest on the moist and least on the dry sites, the decrease from 1957 to 1967 was sharpest on the medium moist sites.

The basal area of stems of minor species decreased regularly on all moisture sites until 1967 (Fig. 6). Although the number of stems of minor species increased sharply from 1967 to 1977 (Fig. 2), the new stems were too small to produce an equally marked increase in basal area (Fig. 6).

On all tracts the basal area increased regularly until 1957 with the greatest increase in Cabin, the oldest tract (Fig. 7). From 1957 to 1967 the increase in basal area continued on the Turkey Hill tract, but basal area decreased on the other tracts, especially Cabin. Then, from 1967 to 1977 the basal area on Turkey Hill scarcely changed, while on the other three tracts the increase in area resumed. The basal area of minor species decreased steadily on all tracts during 1927-67 (Fig. 8). During 1967-77 it continued to decrease on Turkey Hill, but increased slightly on the other tracts in response to increased numbers.

Turning to the differences among species, one finds that despite the considerable changes in numbers of stems, the proportion of the basal area contributed by species was surprisingly steady (Table 4). An increase in the basal area of red and black oak compensated for a decrease in chestnut and white oaks, keeping the total contribution of oaks at about 40 percent of the basal area, while their contribution to the number of stems was declining sharply. On the other hand, while birch and maple were increasing their contribution to the number of stems, their proportion of the basal area scarcely changed during the half century. Tulip poplar, which contributed a small proportion of the stems, steadily increased its proportion of the basal area and now contributes 6 percent. Although its contribution is small, beech steadily increased its basal area. In contrast, white ash contributed less each decade. After a half century there is scarcely any contribution to basal area by pioneer species. The minor species contribute less than 2 percent of the basal area. Only chestnut increased its proportion of the basal area, and that proportion is still small.

The effect of the site upon basal area of species was explored as we had explored the effect of site on the population of species. That is, we calculated the deviations of the percentage of species from the mean percentage of basal area contributed by each species for each moisture class and year.

On the moist sites in 1927 the forest was relatively rich in the basal area of red maple and yellow birch and poor in five oak species. A half century later much the same description applied.

On the medium moist sites in 1927 the forest was rich in red oak and poor in red maple, and in 1977 it remained the same.

On the dry sites the half century began with the forest rich in white and black oak and poor in red maple and yellow birch. It ended rich in black and scarlet oak and black birch and poor in red maple, yellow birch, and tulip.

In the proportion of basal area the outstanding differential changes among moisture classes during the half century were:

Black oak gained on medium moist and dry sites, and white oak lost.

Chestnut oak lost on medium moist sites.

Black birch gained on dry sites.

Tulip gained on moist and medium moist sites.

DISTRIBUTION OF DIAMETER

To analyze the changing diameter of stems in the forest we classified their diameter, breast high, into four classes: small sapling, 0.5 to 1.5 inches; large sapling, 1.6 to 5.5 inches; pole, 5.6 to 11.5 inches; sawtimber, larger than 11.5 inches.

The distribution of diameters of major species is depicted in Fig. 9. The scale of Fig. 9 is logarithmic so that

Table 4. Basal area of major and minor species (percent of total), all tracts. The letter i indicates 0.1 to 0.9 percent and Q indicates the species is present but less than 0.1 percent. Sum over all moisture classes includes trees on muck.

Major Species	Moist					Medium Moist					Dry					All				
	1927	1937	1957	1967	1977	1927	1937	1957	1967	1977	1927	1937	1957	1967	1977	1927	1937	1957	1967	1977
Sugar maple	5	5	5	6	7	1	1	2	2	2	i	i	i	i	i	2	2	2	3	3
Red maple	24	24	20	22	22	11	10	10	12	14	11	10	7	8	10	15	14	12	14	15
Red oak	7	10	17	17	16	14	17	23	25	24	9	12	17	20	20	12	15	21	22	22
Black oak	2	2	2	2	3	4	6	8	8	9	12	16	21	20	18	5	6	8	9	9
Scarlet oak	2	3	3	2	2	5	6	7	7	6	8	10	12	12	12	5	6	7	7	6
White oak	2	2	2	1	1	10	10	8	5	4	16	17	14	7	7	9	9	8	4	4
Chestnut oak	3	5	6	3	1	8	9	9	4	3	4	3	4	3	3	7	7	8	4	3
Yellow birch	15	16	16	17	16	7	7	6	6	7	1	i	i	i	i	8	8	7	7	8
Black birch	11	8	10	12	14	13	13	13	15	16	16	16	16	20	23	13	12	13	15	16
Paper birch	0	0	0	0	0	i	i	i	i	i	0	0	0	0	0	i	i	i	i	Q
Bitternut hickory	i	i	0	0	Q	Q	Q	Q	Q	Q	0	0	0	0	0	Q	Q	Q	Q	Q
Mockernut hickory	i	Q	Q	Q	Q	1	i	1	i	i	1	1	1	i	i	i	i	i	i	i
Pignut hickory	i	i	i	Q	Q	2	2	2	2	i	5	4	3	2	i	2	2	2	2	i
Shagbark hickory	i	i	1	1	1	1	1	i	i	i	i	i	i	i	i	i	i	1	i	i
Beech	i	i	i	1	2	i	i	i	1	2	i	i	1	2	3	i	i	i	1	2
Tulip	2	3	4	6	7	3	4	4	6	7	i	i	i	i	1	3	3	4	5	6
White ash	5	5	5	5	5	4	4	3	3	2	2	2	i	i	0	4	4	3	3	2
Black ash	i	i	0	0	0	Q	Q	0	0	0	0	0	0	Q	0	i	i	Q	i	i
Basswood	i	i	i	0	0	i	i	i	i	i	0	0	0	0	0	i	i	i	i	i
American elm	2	2	2	i	Q	Q	Q	Q	Q	Q	Q	0	0	0	0	i	i	i	i	Q
Bigtooth aspen	5	4	0	0	0	2	2	i	Q	0	3	1	0	0	0	3	2	Q	Q	0
Quaking aspen	Q	Q	0	0	0	0	0	0	0	0	0	0	0	0	0	Q	Q	0	0	0
Pepperidge	i	i	i	i	i	i	i	i	i	i	Q	Q	0	0	0	i	i	i	i	i
Black locust	0	0	0	0	0	0	0	0	0	0	Q	Q	i	i	i	Q	Q	Q	Q	Q
Butternut	i	Q	0	0	0	i	i	0	0	Q	i	i	0	0	0	i	i	0	0	Q
Black cherry	i	i	Q	0	0	i	Q	0	0	Q	i	Q	0	0	0	i	Q	Q	0	Q
Sassafras	i	i	i	i	Q	i	i	i	i	i	i	i	i	i	i	i	i	i	i	i
White pine	0	Q	0	0	0	i	i	Q	Q	Q	0	0	0	0	0	i	i	Q	0	Q
Hemlock	Q	Q	Q	i	i	Q	Q	Q	Q	i	0	0	0	0	0	Q	Q	Q	Q	i
Redcedar	0	0	0	0	0	i	Q	Q	0	0	i	0	0	0	0	i	Q	Q	0	0
Square feet/acre	76	90	102	99	102	64	84	99	90	98	47	68	85	81	90	63	82	97	90	97
Minor Species																				
Chestnut	Q	Q	Q	Q	0.1	0.1	Q	0.2	0.3	0.4	0.3	Q	0.2	0.3	0.6	0.1	Q	0.2	0.3	0.4
Dogwood	0.3	0.2	0.3	0.4	0.5	1.2	1.0	0.9	1.0	1.1	0.5	0.4	0.2	0.3	0.3	0.9	0.8	0.7	0.8	0.9
Shadbush	0.3	0.4	Q	Q	Q	0.2	0.2	Q	Q	Q	0.4	0.4	0.2	0.2	0.1	0.3	0.2	Q	Q	Q
Hophornbeam	1.2	1.0	0.7	Q	Q	0.9	0.6	0.4	Q	Q	0.6	0.4	0.2	Q	0	0.9	0.6	0.4	Q	Q
Gray birch	4.7	2.8	0.1	0	0	4.0	2.4	Q	Q	0	4.4	2.2	0	0	0	4.2	2.4	Q	Q	Q
Witchhazel[1]	1.0	0.7	0.9	0.8	0.8	0.9	0.7	0.5	0.4	0.5	0.3	0.1	Q	Q	0.1	0.9	0.6	0.5	0.5	0.5
Bluebeech	3.3	2.5	1.9	0.6	0.2	2.5	1.5	0.7	0.2	0.1	1.4	0.5	0.1	Q	0	2.5	1.5	0.8	0.3	0.1
Square feet/acre	9.1	7.4	4.3	2.0	1.7	6.9	5.7	2.7	1.9	2.2	4.1	2.9	0.9	0.7	1.0	6.8	5.5	2.7	1.7	1.9
All species	85	97	107	101	104	70	90	102	92	100	51	71	86	82	91	70	88	99	92	99

[1] Witchhazel not measured on Turkey Hill in 1927.

the few but important sawtimber stems and poles are not overshadowed by the numerous saplings.

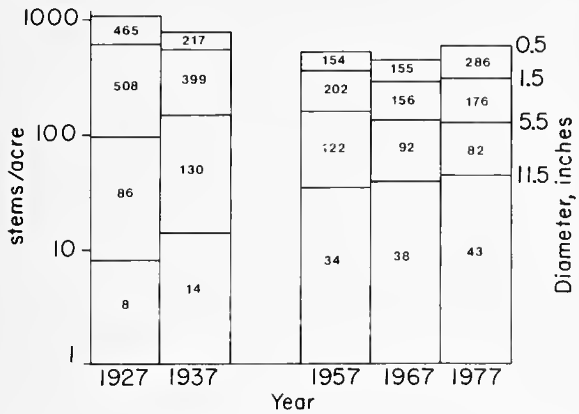

Fig. 9. Diameters of major species. On a logarithmic scale, the number of stems/acre with diameter greater than 0.5, 1.5, 5.5 and 11.5 inches.

The strongest impression gained from Fig. 9 is the slow and steady increase in sawtimber stems -- even during the defoliation of 1957-77. The intermediate class of poles has failed to increase in number. As expected the number of saplings decreased steadily -- until small trees grew during the defoliation of the last two decades.

Minor species, of course, remained mostly saplings (Table 5). While the number of small saplings fell to less than half during 1927-67, the number of big saplings fell to less than a quarter. Thus instead of recruiting from the smaller class and increasing, the bigger class of saplings was shrinking. And when new stems appeared following the defoliation of 1957-67, the increase of small saplings was a quarter, but of big saplings, only a tenth. Apparently, loss of gray birch, hophornbeam and bluebeech, all capable of becoming large saplings or small poles, and the relative increase in witchhazel, dogwood and the short-lived chestnut brought about this shift from large to small saplings. Evidently the minor species are doomed to remain minor.

For major species the pattern of change was similar on all moistures. The proportion of small saplings declined during 1927-57 but increased thereafter. Large saplings declined steadily during 50 years. Poles increased until 1957 but then declined, especially on medium moist and dry sites. The proportion of sawtimber trees increased gradually until 1967 and then declined slightly. However, the decrease is due to an increased number of trees rather than loss of sawtimber (Fig. 9). The decrease of large saplings and poles was not caused solely by growth to larger classes. We conclude that mortality has been greatest in these two classes (Table 5).

Among the tracts the pattern of change among diameter classes of major species was similar to the average over all tracts. Except on Turkey Hill, the proportion of poles increased until 1957 and then declined. During 1937-77 the proportion of large saplings declined while the proportion of small saplings increased on all tracts except Turkey Hill.

In the average over all species, moistures and tracts less than 1 percent of the stems were sawtimber in 1927; by 1977 there were 7 percent. Oaks gained rapidly in sawtimber; in 1977 nearly two-thirds of red, black and scarlet oak and a quarter of white and chestnut oak were sawtimber. About a tenth of hickories and white ash were sawtimber. Although not numerous, a third of the tulip was sawtimber in 1977. In contrast, the maples and birches changed little; although they are becoming numerically important in the forest (Table 2), fewer than 5 percent became sawtimber by 1977.

MORTALITY

Since the changes in these forests are "natural" and since the tracts were covered by a canopy of fifteen hundred small trees per acre in 1927, the growth of some trees meant others naturally fell behind and died in the shade. Also, insects and diseases took a toll.

The net change in the number of stems is shown in Figures 1 and 2. The net difference between decades is the newly appearing minus those dying. The net does not show how the change was caused. For if the number dying is near the

Table 5. Diameter class distibution (percent of total for the year), all tracts and moistures. (Small saplings, 0.5-1.5 inches; large saplings, 1.6-5.5 inches; poles, 5.6-11.5 inches; sawtimber, greater than 11.5 inches.) The letter i indicates 0.1 to 0.9 percent.

Species	Small Sapling					Large Sapling					Pole					Saw Timber				
	1927	1937	1957	1967	1977	1927	1937	1957	1967	1977	1927	1937	1957	1967	1977	1927	1937	1957	1967	1977
Sugar maple	61	54	49	43	40	35	40	44	47	49	4	6	7	8	9	i	i	i	1	2
Red maple	52	37	39	41	51	44	54	46	42	34	4	9	14	16	13	i	i	i	1	1
Red oak	33	15	6	5	7	52	52	28	10	7	13	29	42	35	24	1	4	24	49	63
Black & scarlet oak	21	12	3	2	9	58	42	14	2	3	20	41	55	38	22	1	5	28	58	67
White & chestnut oak	42	24	16	14	40	48	52	27	24	8	10	21	44	38	29	i	3	13	24	23
Yellow birch	43	29	36	41	59	48	54	44	37	28	8	15	17	18	11	i	2	3	3	2
Black birch	41	26	29	33	45	49	56	40	36	33	9	17	26	25	18	1	2	5	5	4
Hickories	53	30	15	13	36	43	59	55	38	30	4	10	29	46	25	i	i	1	4	9
Beech	70	59	59	51	54	29	39	38	46	40	1	2	2	3	5	0	0	i	i	i
Tulip	18	8	5	4	47	50	30	14	8	8	29	49	41	31	12	3	13	39	58	34
White ash	45	26	28	25	29	51	62	43	26	14	3	11	27	46	46	i	i	2	3	11
All major	44	29	30	35	49	48	52	39	35	30	8	17	24	21	14	i	2	7	9	7
All minor	71	62	76	82	84	28	37	24	18	16	i	i	i	i	i	0	0	0	0	0

Table 6. Mortality (percent), all tracts. Sum over all moisture classes includes trees on muck.

Major Species	Moist				Medium Moist				Dry				All			
	1927 to 1937	1937 to 1957	1957 to 1967	1967 to 1977	1927 to 1937	1937 to 1957	1957 to 1967	1967 to 1977	1927 to 1937	1937 to 1957	1957 to 1967	1967 to 1977	1927 to 1937	1937 to 1957	1957 to 1967	1967 to 1977
Sugar maple	12	34	14	15	20	31	13	12	19	31	20	8	17	32	14	13
Red maple	31	45	25	22	32	48	18	16	35	51	19	14	32	48	19	16
Red oak	29	39	45	39	34	45	40	24	31	45	28	12	33	44	39	24
Black oak	35	55	60	0	29	41	34	6	26	50	38	22	28	45	36	12
Scarlet oak	6	50	38	0	29	25	33	28	15	38	36	5	24	31	34	20
White oak	51	61	67	25	45	73	63	39	28	69	72	25	42	71	66	35
Chestnut oak	10	59	27	25	31	42	55	39	41	46	29	21	30	45	51	35
Yellow birch	25	35	23	32	30	44	30	17	33	56	12	11	28	41	27	21
Black birch	22	35	12	15	27	43	17	20	25	40	10	14	27	42	15	18
Paper birch					29	17	29	60					29	17	29	60
Bitternut hickory	50	100			53	78	50	0					52	82	50	0
Mockernut hickory	57	67	0	0	31	44	58	65	19	52	50	83	29	47	55	67
Pignut hickory	33	62	80	0	53	64	50	57	39	72	59	92	48	67	54	64
Shagbark hickory	21	18	40	14	30	30	38	70	18	67	75	0	28	33	41	55
Beech	67	33	0	9	24	47	8	6	14	41	8	0	22	45	7	5
Tulip	11	53	22	0	24	45	9	2	50	0	0	0	23	46	11	2
White ash	35	56	39	27	42	67	44	53	24	83	86	100	40	66	42	45
Black ash	25	100	0	0	75	100						100	44	80	0	33
Basswood	17	67	100		46	64	60	0					41	65	41	0
Elm	36	46	47	83	42	62	33	100	100				40	49	39	85
Bigtooth aspen	37	100			31	92	25	100	64	100			40	96	25	100
Quaking aspen	0	100											0	100		
Pepperidge	30	28	15	5	34	52	20	18	60	0	50	0	36	40	19	11
Locust									67	0	0	0	67	0	0	0
Butternut	83	100			81	100			80	100			81	100		
Black cherry	83	89	100		85	100			93	100			85	94	100	
Sassafras	58	75	53	71	49	67	40	51	69	44	25	19	54	65	42	48
White pine		100			0	100	100						0	100	100	
Hemlock	0	0	0	0	0	0	0	0					0	0	0	0
Redcedar					93	50	100		100				94	50	100	
All major	31	45	26	23	35	50	28	20	32	53	27	16	34	50	27	20
Minor Species																
Chestnut	100	100	40	80	92	78	50	81	94	80	57	78	93	80	51	80
Dogwood	33	17	12	17	28	51	19	20	35	64	8	31	29	50	18	20
Shadbush	34	91	50	50	29	91	79	50	48	84	25	50	34	90	60	54
Hophornbeam	51	38	92	50	51	52	86	50	32	50	100	0	50	50	89	47
Gray birch	62	97	100		62	97	83	100	59	100			61	98	88	100
Witchhazel[1]	58	46	46	36	50	55	43	35	59	48	43	21	52	53	44	34
Bluebeech	47	65	66	74	51	73	73	62	46	80	95	100	50	71	71	67
All minor	51	61	55	45	50	66	50	46	55	75	61	59	51	65	52	47

[1] Witchhazel not counted on Turkey Hill in 1927.

number appearing, the net change will be small, and the turnover within the population will be overlooked. Thus we examined mortality.

Table 6 shows the mortality of each period as a percent of trees alive at the beginning of a period. Because the second interval, 1937-57, spanned two decades, the mortality per decade is roughly half the tabular value.

During the half-century, the mortality of major species per decade decreased slightly, falling from about a third to a fifth. The slight decrease from the first to the last decade occurred on all moisture classes.

The mortality of minor species was a half to a third per decade, somewhat greater than in the major species. The mortality of the minor species was somewhat greater on the dry sites than on others.

The area of muck was slight and the mortality must be calculated with a sample of only about fifty trees. About a quarter of these died each decade, much as on the other sites.

No tract was average in mortality. Cox, with most stems per acre in 1927, had above average mortality, especially of minor species, during 50 years. Conversely, Turkey Hill, with fewest stems

in 1927 had the least mortality during five decades. Reeves and Cabin, intermediate in stem numbers in 1927, were intermediate in mortality during 1927-77. Mortality of major species was slightly above average on Reeves and below on Cabin; mortality of minor species was below average on both.

Among the species, mortality differed. The species that have increased greatly, yellow and black birch and red maple, had less than average mortality. The higher mortality of the oaks is clear. White oak, especially, suffered above average mortality since 1927. Mortality of other oaks exceeded the average only since 1957. Mortality of bitternut and pignut hickory was high, while that of mockernut and shagbark hickory was above average after 1957. Mortality of white ash was above average and accelerated after 1927. Beech, tulip and hemlock slowly made their way into the forest, and their mortality was low. The high mortality of the pioneering aspen, black cherry, sassafras, white pine and redcedar is evident.

The minor species of bluebeech had a high mortality that decreased its role in the understory. Gray birch was eliminated by high mortality, while flowering dogwood and witchhazel, with lower mortalities, gained.

Dutch elm disease and chestnut blight affected the plots. Chestnut blight was present in the tracts in 1927 and mortality removed 40 to 90 percent of the stems each decade. Dutch elm disease, on the other hand, arrived in Connecticut after 1927, and thus one sees in Table 6 a steady increase in mortality of elm.

Our analysis of mortality shows only that trees died. We do not know whether they were little or large. We must await our analysis of growth. First, however, we shall examine the newcomers, called ingrowth.

INGROWTH

Our pursuit of the causes of change causes us to look next at ingrowth because here may lie the future of our forests. Table 7 shows the ingrowth during the half century. Remembering that the tabular value for the double decade 1937-57 is roughly twice the ingrowth per decade, one sees that the ingrowth of major species rose decade by decade from about 50 to 200 stems per acre per decade. This pattern of increase prevailed over all three moisture classes shown in Table 7 (On the small area of muck, the greatest ingrowth was in the second decade).

The change in ingrowth with time differed among tracts. Whereas for four decades on all tracts ingrowth was 50 to 100 stems per acre, during the final decade it increased to over 200 on three tracts while remaining steadily less than 100 on Turkey Hill. When we come to analyze the mortality of basal area of stems of major species, we shall see that the increase in ingrowth during 1967-77 followed mortality of basal area during the preceding decade. Thus the ingrowth during 1967-77 varied among the tracts as did the mortality of basal area and presumably of overstory in the preceding decade (Fig. 10). Openings in the canopy encouraged ingrowth.

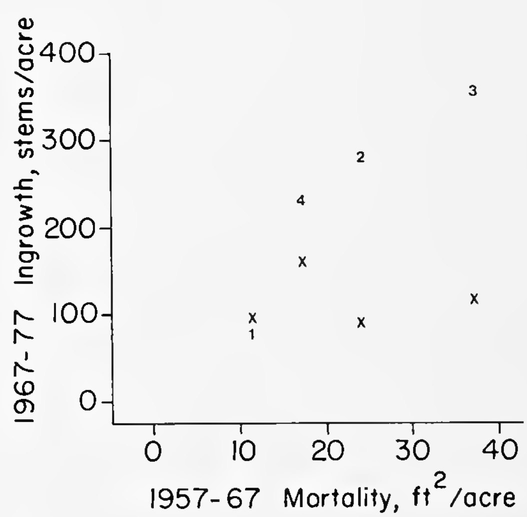

Fig. 10. The ingrowth of major (numbered) and minor (X) species on four tracts during 1967-77 as a function of the mortality of basal area during the preceding decade. Turkey Hill (1), Cox (2), Reeves (3), Cabin (4).

Table 7. Ingrowth (stems/acre), all tracts. The letter *i* indicates ingrowth occurred but was less than 1 stem/acre. Sum over all moisture classes includes trees on muck.

Major Species	Moist				Medium Moist				Dry				All			
	1927 to 1937	1937 to 1957	1957 to 1967	1967 to 1977	1927 to 1937	1937 to 1957	1957 to 1967	1967 to 1977	1927 to 1937	1937 to 1957	1957 to 1967	1967 to 1977	1927 to 1937	1937 to 1957	1957 to 1967	1967 to 1977
Sugar maple	7	24	5	6	3	11	3	6	0	4	0	5	3	12	3	6
Red maple	12	24	10	25	13	42	26	73	11	61	49	99	13	43	26	68
Red oak	7	3	i	2	4	3	i	i	5	4	0	2	5	3	i	1
Black oak	0	0	0	0	1	i	0	1	6	1	i	2	2	i	i	1
Scarlet oak	0	0	0	0	i	i	0	i	0	1	0	0	i	i	0	i
White oak	0	3	0	i	5	3	i	1	8	2	i	2	5	3	i	1
Chestnut oak	4	i	0	2	3	7	i	5	4	3	1	4	3	5	i	4
Yellow birch	18	21	16	93	6	27	14	57	i	3	1	8	7	20	12	56
Black birch	1	10	7	36	7	18	20	48	14	32	29	84	7	18	18	50
Paper birch	0	0	0	0	i	i	0	0	0	0	0	0	i	i	0	0
Bitternut hickory	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	i
Mockernut hickory	0	0	0	2	i	i	i	i	0	0	0	0	i	i	i	i
Pignut hickory	i	0	0	1	1	2	i	i	6	i	i	0	2	1	i	i
Shagbark hickory	0	i	i	0	0	0	0	0	0	i	0	0	0	i	i	0
Beech	1	15	3	13	2	9	8	19	5	12	6	24	2	10	7	18
Tulip	i	i	i	17	0	i	i	3	0	0	0	i	i	i	i	5
White ash	2	9	2	2	2	4	i	1	3	1	0	0	2	5	i	1
Pepperidge	1	1	3	19	i	i	i	2	0	0	0	0	i	i	1	5
Sassafras	0	7	4	9	i	4	7	19	i	2	11	14	i	4	7	16
All major	58	120	51	230	50	129	82	240	63	130	101	246	53	130	79	236
Minor Species																
Chestnut	i	11	2	13	i	41	27	42	2	43	30	80	i	36	23	42
Dogwood	0	6	7	9	8	15	9	23	1	3	1	4	6	12	8	17
Shadbush	3	2	0	2	1	1	i	i	1	i	i	0	2	1	i	i
Hophornbeam	5	16	i	i	1	2	i	2	4	6	i	1	2	5	i	1
Gray birch	0	0	0	0	i	i	0	0	1	0	0	i	i	i	0	i
Witchhazel[1]	48	102	22	60	38	47	26	48	4	8	8	19	34	51	23	45
Bluebeech	12	37	7	13	6	22	3	4	3	9	i	2	6	23	3	5
All minor	69	173	39	98	55	128	66	119	16	69	41	106	51	127	57	112

[1] Witchhazel not counted on Turkey Hill in 1927.

The ingrowth of minor species was about 50 per acre per decade, increasing to about 100 in the last decade. The pattern was similar on all moisture classes. Although the differences of ingrowth among the tracts were less dramatic for minor species than for major, the ingrowth of the minor species on Turkey Hill and Cox in the last decade was less than on the other two tracts.

In 1967 we noted that a substantial crop of red oak seedlings had appeared, especially on Cabin, but they were still smaller than a half-inch diameter and hence did not appear as ingrowth. At that time we wondered what the fate of these seedlings would be, saying these seedlings might play an important role in maintaining the predominance of oak in these forests -- or they might merely stagnate and die in the shade of established larger competitors. In 1977 on Cabin nearly 24 oak stems per acre had grown to a half-inch, but only two were red oak. Over all tracts and sites only one red oak per acre grew to a half-inch while the total for all oaks was eight. Apparently, most of the 1967 red oak seedlings scarcely grew or they disappeared. Many new red oak seedlings appeared in 1977, but the fate of the 1967 crop gives us little hope for the success of the 1977 crop.

GROWTH

In Fig. 5, we saw that the basal area of major species increased until 1957, decreased slightly for a decade and then increased again to the level of 1957. This, however, is net change and the causes are hidden. To learn the causes we can consider basal area as a bank account. From the balance on hand, the initial basal area, we deduct withdrawals. That is, mortality. The remainder

accrues interest called "growth". To this we add the deposits, ingrowth. If we conserve our capital and accumulate the interest, our balance will increase regardless of whether we deposit ingrowth. If however, we squander our capital on mortality and deposit little, then surely our balance will decline.

From mortality (Table 6) we know that trees have died, and at times many, but we do not know whether they were small or large. We already know that ingrowth was less than 100 stems per acre per decade until the last decade. We know nothing of the interest on the balance, growth. Now, in Table 8, we analyze the account in detail.

On all moisture classes the growth (GRO) of major species in the first decade was about 27 ft^2 per acre and since has been about 16 (Table 8). Ingrowth (INGRO) was less than 1 per decade until the last decade when it approached 3. Mortality (MORT) subtracted about 10 per decade except in the fourth decade when it subtracted about 20. The net gain consequently was about 20 ft^2 per acre in the first decade and 7 per decade afterwards except a loss of 7 during the fourth decade.

A surprise is turned up by the analysis of the components of growth. During the half century, basal area increased most on the dry sites. The cause of the greater increase in basal area was not faster growth of stems present for that was greater on moist and medium moist than on dry sites. Neither was the cause greater ingrowth for it was always small. Rather, the advantage of the dry sites was always having less mortality than other sites.

The mortality of minor species exceeded growth and ingrowth, making the net a loss in every decade but the fifth.

Our discussion of growth has so far blended all species together. There were, however, differences among species, and examples are shown in Table 8.

Red maple, one of the three species contributing more than 10 ft^2 per acre to the basal area, increased 1 to 2 ft^2 in most decades. The growth on existing stems was particularly great on the moist site, but this was countered by heavy mortality. Red oak, which contributes the most basal area of any species, increased rapidly in basal area for three decades, but has scarcely changed for the last two. It suffered great mortality on moist and medium moist sites. White oak was a particularly heavy loser with slow growth and great mortality causing net losses in basal area for forty years. Black birch stems added less to their basal area than did the red oaks, but few died and the basal area of birch nearly doubled after 1927.

Several species that do not contribute much to basal area are nevertheless interesting. The basal area of tulip increased because of its low mortality. The same is true of beech. The ingrowth of chestnut was twice the growth on existing stems but high mortality kept the net increase in basal area less than 0.2 ft^2 per decade.

COMPOSITION OF THE CANOPY

The landscape, the view of the forest from afar, is the canopy of dominant and codominant trees. This canopy is also important to the working of the forest as it is to our eyes. These tall trees absorb the lion's share of the life-giving light, passing only flecks and diffuse light down to the saplings beneath, and only after death letting candidates emerge into the sun. Although the canopy is wholly the forest seen from afar, it is only a sixth to a tenth of the trees on the tracts, and the number in the canopy, the dominant and codominant trees, decreased steadily on all moisture classes (Table 9).

Only in young stands with short trees can minor species play a role in the canopy. Hence, in 1927 minor species provided about a sixth of the individuals in the canopy, but they were almost absent thereafter.

From the beginning in 1927 the oaks were the most numerous genus in the canopy (Table 9). They furnished about 45 percent of the canopy in both 1967 and 1977. By 1977, the contribution of maples and birches together had risen to

Table 8. Growth of basal area (ft^2/acre), all tracts. GRO is basal area increase on trees present throughout the period; INGRO is basal area of trees appearing for the first time during the period; MORT is the basal area of trees dying during the period (diameter at the beginning of the period); NET is net change in basal area, NET = GRO + INGRO − MORT. The letter Q indicates less than 0.1 but more than zero. Sum over all moisture classes includes trees on muck.

Species	Decade	Moist GRO	Moist INGRO	Moist MORT	Moist NET	Medium Moist GRO	Medium Moist INGRO	Medium Moist MORT	Medium Moist NET	Dry GRO	Dry INGRO	Dry MORT	Dry NET	All GRO	All INGRO	All MORT	All NET
Red maple	1	4.8	0.1	2.3	2.6	2.4	0.1	1.0	1.5	2.0	0.1	1.2	1.0	2.8	0.1	1.2	1.7
	2&3	6.4	0.1	8.4	-1.9	2.7	0.4	2.6	0.5	1.0	0.2	2.2	-0.9	3.2	0.4	3.9	-0.3
	4	3.7	0.2	2.7	1.1	2.2	0.2	0.8	1.5	1.4	0.2	0.8	0.8	2.5	0.2	1.2	1.5
	5	3.8	0.4	4.0	0.2	3.0	0.7	1.2	2.5	2.3	0.4	0.8	1.9	3.1	0.6	1.7	2.1
Red oak	1	4.6	0.1	0.4	4.3	6.3	Q	0.9	5.5	4.4	Q	0.3	4.1	5.7	Q	0.7	5.0
	2&3	9.3	Q	1.4	7.9	10.0	0.2	2.7	7.4	7.5	Q	2.0	5.6	9.4	0.1	2.4	7.2
	4	3.0	Q	4.2	-1.1	3.7	Q	4.0	-0.2	3.0	0	1.1	2.0	3.5	Q	3.5	-Q
	5	2.6	Q	3.3	-0.7	3.4	0.1	2.7	0.8	2.9	Q	1.4	1.4	3.2	Q	2.6	0.6
White oak	1	0.7	0	0.2	0.5	2.5	Q	1.0	1.6	4.7	Q	0.6	4.2	2.4	Q	0.8	1.7
	2&3	0.6	Q	0.4	0.2	2.4	0.2	3.0	-0.4	3.1	Q	3.3	-0.2	2.2	0.1	2.6	-0.3
	4	0.2	0	1.1	-0.9	0.6	Q	4.3	-3.7	0.6	Q	7.0	-6.4	0.5	Q	4.1	-3.5
	5	0.2	Q	Q	Q	0.5	Q	0.6	-0.1	0.5	0.4	0.6	0.3	0.4	Q	0.5	-Q
Black birch	1	2.1	Q	3.3	-1.2	3.8	Q	1.4	2.5	4.3	0.1	1.2	3.1	3.5	Q	1.6	1.9
	2&3	3.5	0.2	0.5	3.2	4.2	0.2	3.3	1.2	4.4	0.2	1.7	2.9	4.0	0.2	2.5	1.7
	4	2.0	Q	0.6	1.4	2.2	0.2	1.5	0.9	3.0	0.2	0.7	2.5	2.2	0.2	1.2	1.2
	5	2.0	0.5	0.8	1.7	3.1	0.6	1.7	2.0	4.4	1.1	1.3	4.2	3.0	0.6	1.4	2.2
All major	1	25.4	0.5	11.7	14.2	27.7	0.6	7.7	20.6	27.2	0.5	6.6	21.1	27.0	0.6	8.2	19.4
	2&3	36.0	1.0	24.6	12.5	35.1	1.7	22.2	14.7	31.3	0.7	15.4	16.6	34.4	1.6	21.8	14.2
	4	15.8	0.7	20.1	-3.7	15.0	0.7	24.0	-8.3	13.5	0.4	17.8	-3.9	15.0	0.7	22.2	.5
	5	16.9	2.2	15.5	3.7	17.4	2.8	13.0	7.2	15.5	3.3	10.2	8.6	17.0	2.8	13.0	6.8
All minor	1	1.7	0.6	4.0	-1.7	1.2	0.4	2.9	-1.2	0.6	0.1	1.9	-1.2	1.2	0.4	2.9	-1.3
	2&3	1.0	1.0	5.0	-3.0	0.6	0.6	4.2	-3.0	0.2	0.3	2.5	-2.0	0.6	0.7	4.0	-2.8
	4	0.4	0.2	3.0	-2.4	0.4	0.2	1.4	-0.8	0.2	0.1	0.5	-0.2	0.3	0.2	1.6	-1.0
	5	0.4	0.4	1.0	-0.2	0.5	0.5	0.7	0.3	0.3	0.4	0.4	0.3	0.4	0.5	0.7	0.2

equal that of oaks, and white ash and tulip contributed a tenth.

Although the same names led the list of contributors to the canopy throughout the half century, some changes were significant. Maples increased their large contributions on moist and medium moist and quickly and nearly disappeared from dry sites. The contribution of white and chestnut oak on medium moist sites fell to half after the defoliation of 1957-67, and black birch gained on the medium moist and lost on the dry sites. Tulip steadily increased its small contribution on all sites.

The preceding paragraphs tell what happened to the number of stems contributed to the forest canopy by each species. All stems, however, do not contribute equally to the canopy; their crowns differ in size. If an adjustment is made for size of crown then it is possible to estimate what proportion of the canopy is made of leaves from each species.

We did not measure the crown span of each tree, but it is reasonable to assume that crown diameter will increase as stem diameter. Since basal area of the stem approximates crown area of the tree, basal area of dominant and codominant trees can be used to estimate their proportional contribution to the canopy. In what follows when we speak of proportion of the canopy we refer to its estimate from basal area.

Over all tracts and sites although only 10 to 17 percent of all stems participated in the canopy they represented 48 to 79 percent of total basal area. As expected, minor species, because of their generally small stature or short life span, contributed little to the canopy. In 1927 minor species, mostly gray birch, comprised only 5 percent of the area of the canopy despite their 16 percent contribution in numbers (Table 9). Thereafter their contribution was negligible and by 1977 minor species ceased to contribute to the canopy.

Among the major species maples and birches differed little in their contribution during 1927-77. Maples comprised 10 percent of the canopy in 1927 and 11 in 1977; birches began with 18 percent and ended with 17. Oaks, on the other hand, comprised 48 percent of the canopy in 1927, rose to 64 percent by 1957 and then during the final 20 years declined to about 57 percent. Among the oaks there was great difference in change. For 50 years, both red and black oak continued to increase their proportion in the canopy. Scarlet and chestnut oak increased until 1957 and declined thereafter. White oak contributed less to the canopy each decade. Hickories and white ash decreased while tulip doubled its proportion in the canopy, rising from 4 percent in 1927 to 8 in 1977.

If we examine the effect of moisture we find that minor species ceased to participate in the canopy after 1937 on dry and after 1957 on medium moist sites.

On the moist sites maple, oak and birch generally increased participation in the canopy at the expense of other species. The contribution of oak to the canopy in 1977 was 50 percent greater than in 1927 despite a continuing decline after 1957.

On the medium moist sites maple fluctuated, starting and ending the five decades with nearly 9 percent of the canopy. Oak increased gradually from 53 to 61 percent during 50 years. Birch fluctuated slightly, beginning at 17 and ending at 16 percent.

The most dramatic changes occurred on the dry sites. Maple decreased from 6 percent in 1927 to slightly more than 1 percent in 1977. Birch decreased from 20 to 9 percent. Oak, on the other hand, rose from 56 percent in 1927 to 86 percent in 1977, a much greater increase than the average over all tracts and sites.

The situation for our lifetimes is clear. Reporting on 1927-57 Olson (1965) wrote, "On all moisture classes of all tracts...the canopy became increasingly dominated by oaks." A decade later, seeing the decline of oak after the drought and defoliation of 1957-67, we saw a signal of the end of the growing ascendency of oak (Stephens and Waggoner 1970). Now, after another decade, it is clear that the oaks will not become more dominant -- but neither will they soon lose

Table 9. Number of dominant and codominant stems in the canopy (percent of total), all tracts. The letter i indicates 0.1 to 0.9 percent and Q indicates less than 0.1 but more than zero. Sum over all moisture classes includes trees on muck.

Major Species	Moist					Medium Moist					Dry					All				
	1927	1937	1957	1967	1977	1927	1937	1957	1967	1977	1927	1937	1957	1967	1977	1927	1937	1957	1967	1977
Sugar maple	3	3	4	6	9	1	i	i	2	2	0	0	0	0	0	1	1	1	2	3
Red maple	25	30	22	26	25	11	8	8	12	13	11	3	i	2	3	14	12	10	15	16
Red oak	7	12	15	12	12	15	20	23	23	23	12	17	21	23	26	13	18	21	20	21
Black & scarlet oak	3	5	4	3	4	10	13	16	14	16	20	32	43	40	37	10	14	17	15	16
White & chestnut oak	5	7	8	5	4	15	17	18	9	8	15	22	21	14	17	13	15	17	9	8
Yellow birch	12	8	16	18	17	6	5	4	6	5	i	0	0	0	0	6	5	6	7	7
Black birch	5	6	12	12	13	13	14	15	18	18	16	11	6	11	10	12	12	14	16	16
Hickories	i	2	4	3	3	5	4	5	5	2	6	5	6	7	2	3	4	5	5	3
Beech	i	i	i	i	i	i	i	i	i	1	i	i	i	i	2	i	i	i	i	1
Tulip	2	3	3	3	4	3	5	4	5	6	i	i	i	i	2	3	4	3	4	5
White ash	5	7	7	10	9	5	4	3	4	4	2	3	0	i	0	5	4	3	5	5
Other major	15	15	3	i	0	4	4	i	i	i	6	2	i	i	i	7	6	1	1	i
All major, stems/acre	216	145	113	113	90	209	147	118	100	81	212	117	94	83	73	210	142	113	101	82
Minor Species																				
Gray birch	16	3	i	0	0	10	5	0	0	0	11	4	0	0	0	11	4	Q	0	0
Other minor	i	i	i	i	0	i	i	i	0	0	i	0	0	0	0	i	i	i	i	0
All minor, stems/acre	41	5	2	i	0	26	8	i	0	0	27	4	0	0	0	28	7	i	i	0

Table 10. Single stems (percent of total), all tracts. Sum over all moisture classes includes trees on muck.

Major Species	Moist					Medium Moist					Dry					All				
	1927	1937	1957	1967	1977	1927	1937	1957	1967	1977	1927	1937	1957	1967	1977	1927	1937	1957	1967	1977
Sugar maple	58	62	78	80	82	64	70	69	75	72	44	54	33	50	67	61	67	71	76	75
Red maple	37	39	38	47	48	50	51	51	58	50	35	39	45	45	41	45	47	47	54	48
Red oak	69	61	42	67	62	72	72	65	71	76	70	71	70	76	80	72	71	66	71	75
Black oak	71	82	100	100	100	83	86	89	87	93	80	82	80	84	86	82	84	86	88	91
Scarlet oak	75	73	75	75	75	68	75	80	87	83	90	92	88	90	85	75	80	82	87	83
White oak	78	85	83	100	100	80	79	83	86	84	79	79	69	85	78	80	79	80	87	84
Chestnut oak	70	59	73	100	100	66	58	64	76	94	62	58	65	57	65	66	58	65	75	81
Yellow birch	42	43	41	50	45	41	43	45	47	45	42	44	88	67	26	41	43	45	48	45
Black birch	60	58	75	82	86	63	69	75	76	76	57	60	67	77	72	62	67	74	77	76
Paper birch						43	50	29	60	0						43	50	29	60	0
Bitternut hickory	100	100			100	100	100	100	100	100	100					100	100	100	100	100
Mockernut hickory	71	100	100	100	100	93	96	96	85	90	74	72	67	50	0	88	90	90	78	87
Pignut hickory	100	100	100	100	100	92	93	84	76	72	91	88	85	100	100	92	92	85	82	77
Shagbark hickory	71	73	70	86	100	66	64	65	57	100	82	78	75	100	100	68	67	67	65	100
Beech	67	67	61	62	62	47	49	54	60	72	14	19	37	52	69	39	41	51	59	71
Tulip	61	65	67	75	84	60	52	57	60	70	100	100	100	100	100	60	55	59	63	76
White ash	67	68	57	67	82	67	68	62	66	67	82	77	43	100	0	68	69	62	68	75
Black ash	50	33	100	100	100	100	100							0		78	60	100	50	75
Basswood	17	17	0			15	21	20	50	0						16	20	14	50	0
Elm	85	78	87	100	100	83	88	100	100	0	100	0	0	0	0	86	82	91	92	67
Bigtooth aspen	100	100				91	92	100	100		100	100				96	96	100	100	
Quaking aspen	100	100														100	100			
Pepperidge	91	88	85	77	93	93	90	90	91	87	100	100	100	100	100	100	100	100	100	100
Locust											100	100	100	100	100	100	100	100	100	100
Butternut	100	100				56	67			0	30	0				56	50			0
Black cherry	69	44	100			90	67			100	93	50				80	53	100		100
Sassafras	89	75	60	71	89	93	92	95	92	95	96	100	88	86	100	93	91	86	88	96
White pine		100				100	100	100		100						100	100	100		100
Hemlock	100	100	100	100	100	100	100	100	100	67					100	100	100	100	100	80
Redcedar						100	100	100			100					100	100	100		0
All major	56	55	56	62	65	65	65	63	66	63	64	65	61	64	61	63	63	62	65	63
Minor Species																				
Chestnut	80	0	100	100	50	64	60	89	80	33	69	20	85	91	32	66	44	89	83	34
Dogwood	67	72	64	80	82	49	50	60	70	77	35	32	42	69	64	50	50	60	71	77
Shadbush	18	26	33	50	20	45	42	43	50	40	21	11	0	25	0	34	34	36	46	25
Hophornbeam	72	59	75	100	67	49	43	48	93	79	45	55	56	100	100	52	47	57	95	80
Gray birch	45	33	50			50	45	67	100		54	32			100	49	41	62	100	100
Witchhazel[1]	15	14	16	14	12	16	17	16	14	10	11	17	22	8	0	15	16	16	13	10
Bluebeech	35	31	35	51	59	29	28	37	40	40	17	22	25	100	67	30	28	36	44	47
All minor	35	29	33	36	30	34	31	43	47	35	36	28	56	68	29	35	30	41	46	33
Total	49	47	48	55	56	55	55	57	60	55	59	60	61	65	55	55	54	55	60	55

[1] Witchhazel not counted on Turkey Hill in 1927.

their great role.

SPROUTS

In the forest, trees may grow as single stems or as clumps of sprouts. Clumps of sprouts arise after injury to the original stem. To determine whether the single stems presumably grown from seedlings are intrinsically superior to sprouts, we classified the trees as single stems or sprouts.

All trees that were members, survivors or recruits of a sprout clump were classified as sprouts. The remainder were classified as single stems because they had never visibly been members of a sprout clump during 50 years. Some of these latter trees may have originated as sprouts. Also, a few trees, originally single stems, later became a member of a sprout clump. The percentage of single stems is shown in Table 10.

Over all tracts and moistures the proportion of major species that were single stems varied little from two-thirds during 50 years. Single stems of minor species, however, increased from 35 percent in 1927 to 46 percent in 1967 and then declined to 33 percent in 1977.

Among the moisture classes the proportion of single stems in major species increased from 56 percent to 65 percent in 50 years on moist sites but remained nearly steady at 64 percent on medium moist and 63 on dry sites. Among the minor species the increase in single stems was greatest on dry sites and least on moist. On nearly all moistures the proportion of single stems was different from tract to tract.

It is striking that during a halving of the number of stems of major and minor species the proportion of sprouts remained scarcely changed.

How do individual species or species groups compare? Red maple and yellow birch had less than half of their stems as single stems. In both, the proportion of single stems increased slightly during 1927-67 and then decreased. Oaks, black birch and the hickories had two-thirds or more of single stems, and the proportion increased gradually during 1927-77. For oaks and hickories this increase in proportion of single stems as the number of stems decreased (Table 2) clearly indicates the enhanced survival of single stems.

If single stems are better suited for survival where do they occur in the stand structure? We learned that the proportion of major species stems contributing to the canopy ranged from 14 to 23 percent during 1927-77 (Table 9). However, we have not told whether these stems are sprout or single. Fig. 11 shows the disposition of sprouts and single stems in the canopy and below it. We see immediately that in the canopy single stems outnumber sprouts nearly two to one for all sites and years. Although both decreased during 50 years, single stems decreased only to half whereas sprouts decreased to a quarter of their starting number. The proportion of sprouts in the understory remained relatively constant, about 30 percent. Although single stems and sprouts decreased in the understory, the decrease of single stems relative to sprouts was greater on medium moist and dry sites but not on moist. We conclude then that the survival advantage of single stems over sprouts lies among those stems in the canopy.

HEIGHT

The height of dominant trees at a given age is called the site index and indicates the quality of site for forest growth. In 1957 when the stands were 55 to 70 years old, the average height of the taller trees was 68 feet on the moist and medium moist sites that comprised most of the sample area. This was slightly better than medium quality sites in Pennsylvania (McIntyre, 1933), indicating the the central Connecticut sites were medium or slightly better in quality.

In 1967, however, no increase in the heights could be detected in a sample of trees on Reeves and measurement was abandoned. Evidently the advancing age of the trees, drought and defoliators had allied to slow the growth in height to an indetectable change in a decade.

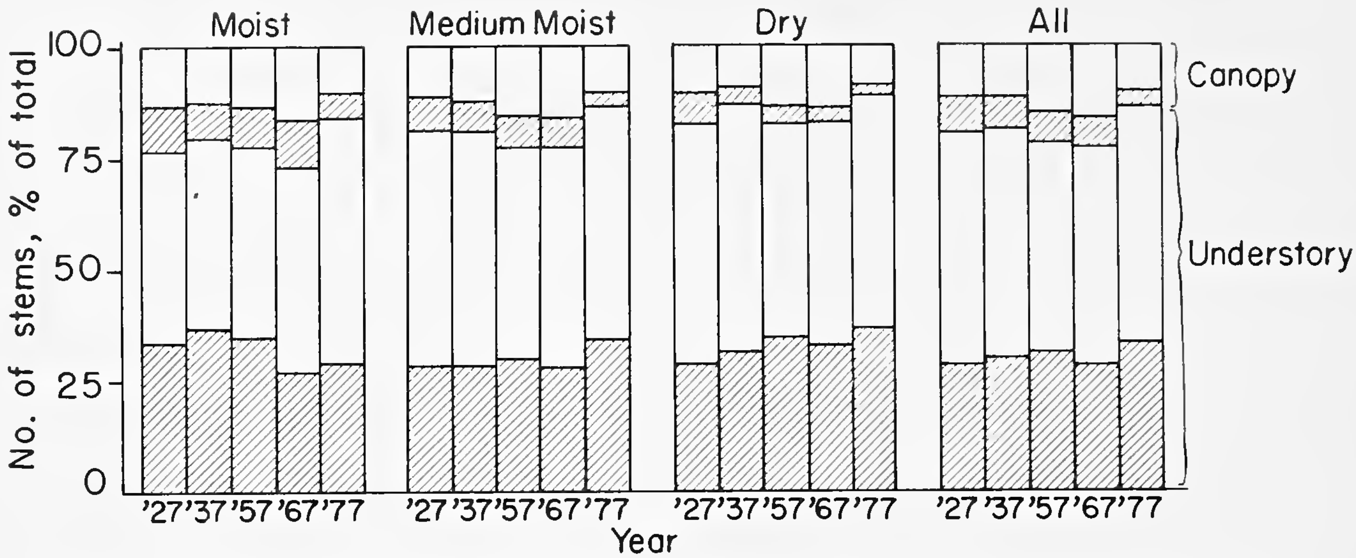

Fig. 11. Distribution of single stems ☐ and sprouts ▨ of major species in the canopy (percent), all tracts. Upper: dominant and codominant trees in the canopy; lower: intermediate and overtopped stems beneath the canopy. All moisture classes includes trees on muck.

In 1977 the merchantable height of trees was measured. These will be reported in a later Bulletin.

FIRE

All results presented so far were from portions of the tracts undisturbed except by hurricane and defoliation. On Turkey Hill, however, there is a portion originally surveyed as part of the tract but disturbed by fire in 1932. The burned portion contains 1.6 acres of transect. Thus by the chance of the fire in 1932 we are able to see first the effect of the wildfires that ravaged so much of our woodland and then 45 years of recovery.

In 1927 the part of the forest that would burn five years later and the part that would escape were similar. Although there was a greater proportion of dry sites on the part that would burn than on the other part, medium moist sites comprised about 70 percent of both (Table 1). Both parts were similarly populated with stems of similar diameter (Table 11 and Fig. 12). Maples and oaks comprised about the same proportions on both. Compared to the remainder, however, the portion destined to burn supported less red maple and yellow birch and more hickories. About 85 percent of the stems were saplings on both portions and 13 percent were poles. The basal area of stems was slightly more on the portion destined to burn than on the other.

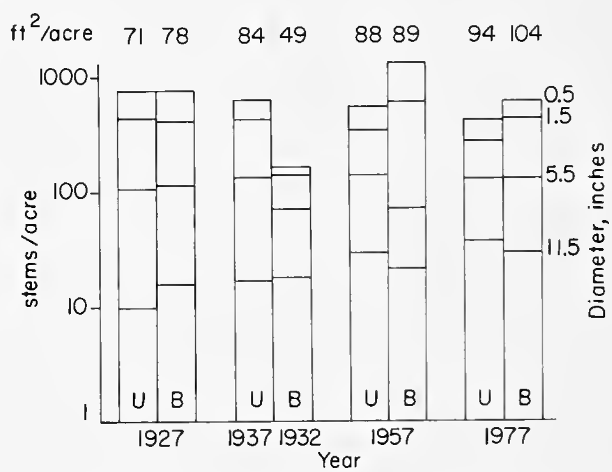

Fig. 12. The Turkey Hill forest that was unburned (U) and burned (B) in 1932. On a logarithmic scale, the numbers of stems/acre with diameter greater than 0.5, 1.5, 5.5 and 11.5 inches. At the top of the graph are shown basal areas of stems in ft^2/acre.

In 1932 fire swept over 1.6 acres and observations were promptly taken. The remainder of the tract was examined in 1937.

The fire eliminated nearly all stems of minor species and more than three quarters of the stems of major, reducing the population drastically (Fig. 12). Although never abundant, redcedar, aspen, basswood, butternut, cherry and sassafras were eliminated. Oak declined by a fourth, hickories declined, and maples and birches increased their proportions by relatively greater survival.

Although 96 percent of small and 82 percent of large saplings succumbed, half the poles and all sawtimber survived. Consequently the basal area decreased by only about a third.

In the unburned portion, as we have seen earlier, the change was much slower. The number of stems declined by only a sixth and basal area increased a fifth in a decade. The relative contributions of the species were stable.

During the following quarter century, 1932-57, the number of stems in the burned forest nearly doubled, and the basal area approached that in the unburned forest. Compared to the unburned portion, ingrowth on the burned was relatively scarce in maple and yellow birch and rich in oak, black birch, hickory, and tulip. Thus fire decimated the population, but the distribution of species changed remarkably little as, for example, maples survived but few grew in.

The abundant ingrowth after the fire completely changed the diameter distribution (Fig. 12). In 1957 about 96 percent of all stems were saplings. Only a few poles grew to sawtimber. Much of the recovered basal area was in the many small stems. Thus in 1957 the burned forest had the population, diameters and basal area of a young stand, resembling Cox or Reeves in 1927 (Fig. 3 and 7).

By comparison, 1937-57 in the unburned forest was a period of slow change. The population decreased only a fourteenth while basal area increased only a tenth.

During the final score of years, 1957-77, the number of stems in the burned forest halved. Mortality exceeded ingrowth several fold. The net effect was an increase in the proportion of red maple and steady or declining proportions of other species. During the score of years, basal area and the number of pole and sawtimber trees grew, while saplings declined.

The large and enduring effects of the fire upon major species were few. Searching the half century of changes, 1927-77, for differences between the unburned and burned forest one finds little to remark. Sugar maple in the unburned caught up to that in the burned: and in the burned, oak declined less, black birch gained more, and hickory lost more than in the unburned. Although a legacy of large saplings was left 45 years after the fire, they will likely disappear in decades to come. Basal area in the burned doubled after the fire and, as in the unburned, increased a third in the century, despite the fire.

So far we have not mentioned the effect of the fire on minor species. In 1927 minor species contributed about a third and a quarter of the stems on the portions that would later be unburned and burned. Dogwood and bluebeech predominated. (Witchhazel was uncounted in 1927.) Minor species contributed less than a tenth of the basal area on both portions.

The fire of 1932 nearly eliminated minor species, leaving only a single witchhazel in the entire 1.6 acres. By 1957, however, their number increased to fully two and a half times their number before the fire with flowering dogwood and witchhazel predominating. During 1957-77 the number of stems and their basal area declined to levels remarkably close to levels in the unburned portion in 1977.

The fraction of the stems that was sprouts was little affected by the fire. On the unburned part of Turkey Hill, the fraction that was sprouts increased slowly and steadily from 38 to 46 percent during the half century. On the burned part, the fraction happened to be half before the fire, fell to 44 percent after the fire, and then rose to 55 percent. In 1927 in the canopy of both parts, about two-thirds of the trees were single stems. In 1977, however, the percentage of single stems in the canopy was only 60

Table 11. Comparison of burned and unburned Turkey Hill forest. The letter <u>i</u> indicates 0.1 to 0.9 percent.

Species	Number (percent major species)						Ingrowth (percent major species)				Basal area (percent all species)					
	Burned			Unburned			Burned		Unburned		Burned			Unburned		
	1927	1957	1977	1927	1957	1977	1932-57	1967-77	1937-57	1967-77	1927	1957	1977	1927	1957	1977
Sugar maple	10	9	14	6	14	19	8	9	19	17	8	6	8	2	2	4
Red maple	10	14	24	17	21	29	14	45	28	36	5	5	7	19	14	16
Red oak	8	9	7	12	9	4	10	1	6	2	6	11	12	5	11	9
Black oak	3	3	4	2	2	2	3	0	i	1	6	5	6	3	6	8
Scarlet oak	3	4	2	2	2	1	4	1	2	i	3	3	3	3	3	2
White oak	8	7	3	6	5	2	6	0	5	0	9	12	11	6	8	7
Chestnut oak	9	12	8	6	6	3	12	6	9	2	10	13	10	7	6	4
Yellow birch	7	4	6	16	16	14	4	13	11	14	8	6	6	16	16	14
Black birch	10	18	17	9	10	11	18	12	4	8	17	19	19	15	14	17
Hickories	13	8	5	5	4	2	8	6	3	2	7	4	3	4	4	2
Beech	2	2	2	3	3	5	2	0	3	4	i	i	i	i	i	i
Tulip	1	4	3	1	1	1	4	0	i	i	2	6	9	3	4	7
White ash	8	2	1	7	4	2	2	0	4	i	5	2	1	3	3	3
Major species, stems/acre	961	1974	885	1075	855	656	1230	42	283	77						
All species, ft^2/acre											78	84	104	71	92	97

in the burned, while it was 80 in the unburned forest. Thus after 45 years the only effect of fire was a small increase in the percentage of sprouts in the canopy.

The fire of 1932 arrested the development of the forest and turned time back fully three decades. Yet the phoenix of the new forest rose from the ashes in four decades, little changed. The treeless state of old field or clearcut forest was not caused by the fire because large trees survived. Twenty-five years after the fire, the forest was a mixture of young and old forest. The many stems, largely saplings, suggested a young forest, but the large basal area suggested an older one. Then, during another 20 years, the burned forest began to behave with maturity: mortality was slowly eroding numbers, and the basal area was slowly increasing as in the portion of Turkey Hill that was unburned.

The fire scarcely changed the distribution among major species. In an analysis of variance we found no significant effect of fire on the change from 1927 to 1977 in the composition of the major species in the forest. However, this need not surprise us. If wildfire prevailed in the past, and it likely did, then selection of species resistant or adapted to fire has likely long since occurred. Indeed, with increased fire protection and prolonged absence of fire, the changes in composition may come in unburned rather than burned forests. Unlike the disturbance of fire, the events treated next are not growing rarer.

DROUGHT AND DEFOLIATION

The period 1957-67 was a decade of drought and defoliation. Although the events were confounded, let us see if their effects can be separated. Turkey Hill was partially defoliated in 1964, 1971 and 1972. Cox, Cabin and Reeves tracts were partially defoliated in 1961, 1962, 1963, 1971, and 1972. Defoliation was severe on Reeves in 1963 and on Cox in 1971. Therefore, we can classify the recorded history of the tracts in the four intervals: 1927-37, a time of moderate drought without defoliation; 1937-57, a moist middle interval spanning two decades without defoliation; 1957-67, a decade of severe drought with light defoliation on Turkey Hill, moderate defoliation on Cox and Cabin, and heavy defoliation on Reeves; 1967-77, a moist decade with moderate defoliation.

The effect of drought and defoliation might be assessed by mortality, ingrowth or growth of the persistent trees. At first glance mortality seems the proper measure because favorable conditions should decrease and unfavorable conditions should increase mortality. Because

mortality (Table 6) changed as the forest aged, however, it is likely a poor indicator. Since ingrowth was small and generally unaffected by site and decade (Table 7), it, too, is useless by itself. The growth or accretion of the basal area of stems living throughout an interval should, on the other hand, reveal the effect of conditions during that interval.

Accordingly, the growth of trees present throughout an interval is presented in Table 12. The growth is the increase in basal area as a percentage of those same trees at the beginning of the interval. Since the second period, 1937-57, is twice as long as the others, we have adjusted the percentages for decades 2 and 3 in the table. If the initial area grows at g per period, the growth in two periods is $((1 + g)^2 - 1)$, and g is tabulated in Table 12.

Generally, growth slowed as the forests aged, the growth of major species decreasing from 43 percent in the first decade to 19 percent in the second and third and to 16 and 19 percent in the fourth and fifth.

If the effect of drought is appraised by growth on lightly defoliated Turkey Hill, it was slight. Growth was as rapid in dry 1957-67 as in moist 1937-57 and 1967-77. The growth of three species on four tracts increased -- but insignificantly -- despite the drought of decade 4.

How can we appraise the effect of defoliation? During 1957-67 the sum of all major species grew less on defoliated Reeves, Cabin and Cox than on lightly defoliated Turkey Hill (Fig. 13). It should be noted, of course, that growth on the defoliated tracts sprang back in the following decade, 1967-77, exceeding the growth on Turkey Hill although Cox was the most severely defoliated in 1967-77. Growth during 1967-77 was unrelated to the defoliation received.

Since species may be more or less delectable to defoliators, an inkling of the impact of defoliation can be sought in a comparison of species. White and red oaks are favorite foods, red maple and black birch are intermediate, and

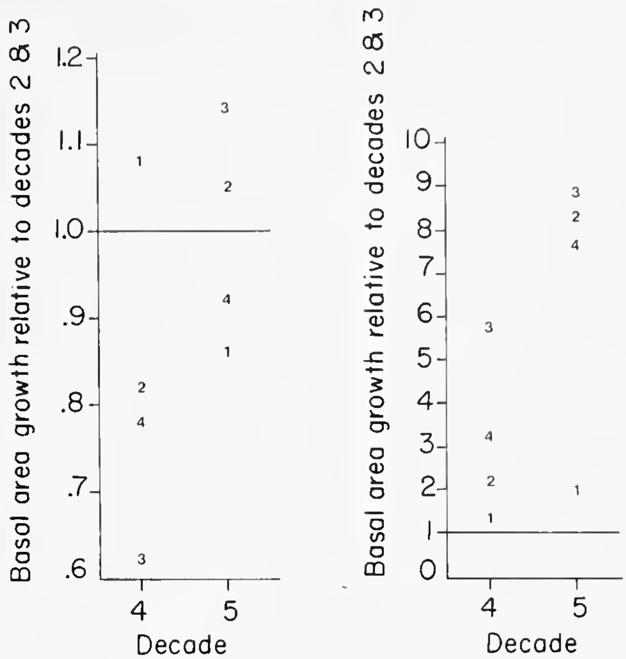

Fig. 13. Growth of major (left) and minor (right) species in decades 4 and 5 relative to growth per decade during decades 2 and 3. During decade 4 trees were defoliated more on Cabin (3) and Reeves (4) while on Turkey Hill (1) and Cox (2) defoliation was less.

tulip is not eaten, and the species are listed from white oak to tulip in Table 12. Clearly tulip poplar grew well in defoliated Reeves during defoliation, decade 4. So, too, did red maple and black birch. The favorite food, white oak, did, however, suffer markedly more on Reeves than on Turkey Hill during 1957-67.

A more thorough analysis was made by relating the growths of decades 2 through 5 to rain, susceptibility of a species to defoliation and defoliation of a tract. The deviation of rainfall from normal was one independent variable. Another was a susceptibility of 0 for tulip, 1 for black birch, 2 for red maple and 3 for red oak. Another was the defoliation of a tract per decade with an added unit for the severity of defoliation of Reeves in 1963 and Cox in 1971. The dependent variable was the deviation of the growth percentage in a decade from the mean for that species over all tracts and decades.

Fortunately for common sense rain had a positive and the product of susceptibility and defoliation had a negative

Table 12. Growth of basal area on residual trees (percent of initial basal area), all moisture classes. Percentage for decade 2 and 3 is adjusted to a single decade.

			——Increasing defoliation——→				
Species	Decade	Burn	Turkey Hill	Cox	Cabin	Reeves	All but burn
White oak	1	10	28	39	46	49	40
	2&3	41	22	10	12	14	13
	4	19	16	4	3	7	7
	5	10	11	6	18	14	10
Red oak	1	14	82	70	64	60	67
	2&3	33	38	30	30	28	30
	4	36	21	17	14	17	17
	5	19	13	16	16	15	15
Red maple	1	7	20	34	30	27	28
	2&3	15	10	15	12	12	12
	4	43	22	24	17	19	21
	5	33	19	28	25	24	24
Black birch	1	11	26	56	50	36	39
	2&3	17	16	21	21	14	17
	4	23	15	24	19	15	18
	5	17	15	35	24	18	22
Tulip	1	24	63	101	50	34	56
	2&3	33	32	41	21	13	26
	4	40	30	27	24	23	26
	5	55	41	36	29	36	35
All major	1	9	32	49	46	43	43
	2&3	21	18	20	19	19	19
	4	29	19	17	12	15	16
	5	20	15	21	22	17	19
All minor	1	1	19	20	12	11	18
	2&3	4	9	4	3	6	5
	4	13	12	8	17	18	12
	5	17	17	32	26	44	26

effect on growth -- but they were insignificant effects.

Finally, we examined the effect of drought and defoliation on the mortality of white oak, which anecdotes have related to defoliation. We examined decades 1 through 5 and used the rain and defoliation variables described above. Again, the outcome was sensible, rain decreasing and defoliation increasing mortality of white oak. Although the effect of rain was significant, adding defoliation did not significantly improve the explanation of the death of white oak.

The conclusion had to be, therefore, that defoliation had a much less dramatic effect on growth during an entire decade than one guessed from the stark bareness of branches in a June when defoliators were at work. This long-term effect contrasts starkly with the high mortality of oak observed one to three years after repeated defoliation (Dunbar and Stephens 1975).

Minor species, growing in the shade of major species on undefoliated Turkey Hill, actually grew about as much during dry 1957-67 as during the moister preceding and following decades (Table 12). Thus drought certainly was no disadvantage to the understory (Fig. 13).

Defoliation actually seems advantageous to the understory. Earlier in a Connecticut wood the understory was observed to benefit from the defoliation of the shading overstory (Collins, 1961). Now, in Table 12, we see that the growth

of minor species on Cabin and Reeves surged up during defoliation, decade 4, and rose further during the following decade. On the tracts where defoliation was less, the growth rose after decade 2 and 3, but the surge during decade 4 was less.

The general conclusion is that the effects of drought and defoliation are remarkably small during a decade. There was no detectable effect of drought on the undefoliated tract. Defoliation decreased the growth of major and increased the growth of minor species -- but far less than one would fear during the outbreak of the insects. Next we shall see that the drought and defoliation of decade 4 and the defoliation of decade 5 little affected the probability of change.

PROBABILITY OF CHANGE

In the Introduction we promised to use the surveys to anticipate the future. Now we shall try.

First, what do we mean by "anticipate"? Consider the example of a tract that is now predominantly covered by Red trees. We do not expect to say whether the tract will surely be covered by White trees a decade hence or surely by Red ones. Rather, we shall attempt to say what the probability is that the tract will be covered by a predominantly Red or White forest. This estimation of probabilities is anticipating the future.

Transition Probabilities

The probabilities of transition can be illustrated by the simple example of a tract that has either a Red or White forest upon it. Suppose that 200 tracts have been classified at the beginning and end of a decade. At the beginning, 100 are Red and 100 are White. At the end, 90 of the Red and 80 of the White remain unchanged, while the remainder have become forests of the other sort. The frequencies can be written thus:

	Beginning	
End	Red	White
Red	90	20
White	10	80

The transition probabilities are then simply:

	Beginning	
End	Red	White
Red	0.90	0.20
White	0.10	0.80

That is, if a tract is covered by a forest that is primarily Red, there are 9 chances out of 10 that it will still be covered by Red a decade later. If these probabilities could be estimated, then we would say that the future of the tract, so far as the predominant tree is concerned, was anticipated.

Foreseeing the future would be difficult if the probabilities changed with time. If, on the other hand, the probabilities were constant, estimating them would be very simple. One would only have to observe them over a suitable interval, such as a decade, and then go on extrapolating them into the future.

For example, the transition probabilities among oak and maple on the tracts will be calculated for the 1927-37 and 1967-77 decades. If they are similar despite the great lapse of time and change in population, the probabilities will be proposed as an anticipation of the future. On the other hand, if the transitions are different from decade to decade they provide a summary of the response of the forest to age and weather but they are poor guides to the future.

Before this investigation is undertaken, the properties of the constant transition probabilities should be identified. If they do not depend upon how the forest got to the state it is in but only upon what state it is in, we are dealing with a Markov chain. If the probabilities do not change as the decades pass, the chain is stationary and has convenient mathematical properties

(Feller, 1950).

One convenient property allows the probability of a change over, say, two decades to be derived from the probability of a change over one decade. To do this, the matrix of probabilities for one decade is simply multiplied by itself according to the rules of matrix algebra.

This operation can be seen easily in the simple example of the Red or White forest. The probability of a Red forest remaining continually Red for two decades is 0.90 x 0.90 or 0.81. But if we observed the forest only at the beginning and end of the two decades, the forest would also seem to remain Red when, in fact, the Red became White in the first and returned to Red in the second decade. The probability of this latter course is 0.10 x 0.20 or 0.02. Therefore, the probability of a Red forest standing on a tract at the beginning and end of two decades is 0.81 + 0.02 or 0.83. If the multiplication is continued for all rows and columns of the matrix, then a new matrix of probabilities is obtained, and it is for the transitions over two decades.

The matrix for two decades can serve two purposes. First, it is an estimation of the change over 20 years that can be derived from observations over ten years. Second, it can be used in testing whether the changes over the single decade of 1927-37 are comparable to those over the double decade of 1937-57.

Another useful characteristic of a Markov chain with constant transition probabilities is seen in estimating the changing states and even the equilibrium or steady state. The estimate of the number of Red plots after one period is (0.9 times 100) plus (0.2 times 100) or 110. After the process is repeated a second time, the number of Red plots becomes 117.

The steady state is also easily calculated. After the transitions have gone on for a long time, individual trees will still be dying and growing into our ken, but the percentage of plots dominated by a certain species, or some other characteristic, will remain near an equilibrium. The simple calculation is easily described with the Red and White species. The reader has just seen that the proportion of Red plots at the end of a period is 0.9 times the proportion of Red plus 0.2 times the proportion of White at the beginning of the period. In algebraic terms,

$$r = 0.9r + 0.2w$$

The second rule says that the sum of the Red and White proportions is 1.0. In algebraic terms,

$$r + w = 1.0$$

The solution of these equations: at equilibrium the proportions will be two-thirds Red and one-third White.

The estimated future states and, especially, the steady state, like all extrapolations, put short-term conclusions to a severe test, revealing some ridiculous ones. If, however, the extrapolation makes common sense, it is an adequate anticipation of the future. Further, the steady state is a summary of the entire matrix of probabilities, telling where they are heading.

Forests have been analyzed before in terms of probabilities. For example, Usher (1966) has set down the recruiting of stems into the smallest class and their transition to larger classes as a matrix of probabilities. Our contribution is in using probabilities in two other ways. First, to analyze changes in kind as well as size of trees. Second, to see whether the transition probabilities are constant from decade to decade, making a stationary Markov chain and easy calculation.

With this introduction to transition probabilities, which are delineated by Ashby (1956) and thoroughly discussed by Feller (1950), the actual frequencies of change in the Connecticut forests are now examined. First, the changes in the predominant species, much as the simple foregoing example of the Red and White classification, are examined. Then the changes in diversity, in stem numbers, and in basal area are investigated.

Each chain or 66-foot length of transect through the forest was considered as a plot of ground where the change over a decade could be examined. It is a sample of the forest seen through a window, and

the viewer wonders how it will change in 10, 20, 40 or 50 years. Since the transects are a rod or 16.5 feet wide, the plots are 1/40 acre. Excluding all tracts wholly burned in 1932 or otherwise disturbed, assigning the chains to the predominant moisture class of the chain, and omitting those on muck, moist and dry sites, a sample of 250 fairly uniform, medium moist plots is left for analysis.

The next task is classifying the trees upon the tracts into a few groups. Only a few classes can be made lest the sample in some classes be too small. Also, the classes must be easily grasped by the reader if they are to convey any information. Finally, good fortune must attend this process, since the constancy of the probabilities depends upon the skill of classification.

Predominant Species

The first classification of the tracts according to predominant species was merely asking which group of species contained the most stems on each of the fortieth-acre plots. It may be said that the most numerous class "dominates." Five species classes were set up: maple, oak, birch, other major species, and minor species. Thus if more stems on a plot were in the maple class than in any other single class, the population on that plot was classified "maple."

The transitions from 1927 to 1937 are tabulated in Table 13. The classes contained reasonably large numbers at the beginning of the decade, ranging from 28 plots in the "other major species" to 68 in the "minor species" class. The transitions would be more frequent with smaller, rarer with larger plots, but we shall stick to the fortieth-acre plots.

The clearest phenomenon was the persistence of the classes, which is seen in the large percentages along the diagonal from upper left to lower right. More than 80 percent of the plots that were maple or birch in 1927 retained the same class in 1937. Therefore, a surprisingly accurate anticipation was, "Whatever predominates at the beginning of the decade will still predominate at the end."

Being transition probabilities, the numbers of Table 13 not only tell how frequently forest stayed as it was but also what else it became. For example, the matrix shows that one oaken plot in seven became maple and that the fourth of the minor species plots that changed were distributed to all other classes. But we want to know how constant these transition probabilities were before applying them to the future, and we turn to the 1967-77 transitions, which are tabulated in the lower part of Table 13.

Table 13. Ten-year transitions in classes of species according to number of stems per plot. "Other" means the most numerous are major species other than maple, oak and birch. Probabilities as percentages. Medium moist sites.

Observed 1937 ↓	1927 Maple	Oak	Birch	Other	Minor
Maple	82	15	13	4	9
Oak	7	70	0	4	4
Birch	4	9	84	7	6
Other	0	0	3	71	4
Minor	7	6	0	14	77
Observed 1977 ↓	**1967**				
Maple	67	12	17	7	13
Oak	0	25	2	0	1
Birch	21	38	63	14	11
Other	4	0	2	50	2
Minor	8	25	16	29	73

At the beginning of the last decade the sample sizes ranged from 14 in other major and 8 in oak to 103 in the maple class. Thus the probabilities for oak and other major species must be taken with a grain of salt. Leaving minor fluctuations aside for the present, one has to marvel at how similar the transitions are for the first and last decade of the survey. After all, a great time has passed. The first decade began when Lindy flew the Atlantic, Coolidge was President, and people traveled over dusty roads in Model T's. And the last decade ended with astronauts on the moon, Jimmy Carter in the White House, and gasoline shortages.

The interesting difference in probabilities between the first and last decade of the half century is for oak.

Oak, which had yielded to something else frequently during the drought and defoliation of 1957-67, continued to yield plots during the following decade of 1967-77.

More detailed analysis of the change in transition of oak is possible in Table 14, which shows the transitions from oak in each period. Since the probabilities must be presented for 20-year transitions for 1937-57, all probabilities are presented as 20-year periods by multiplying each matrix of decadal observations by itself. The declining persistence of oak as the most numerous is clear. Light-seeded birch and the lowly minor species became the increasingly frequent, and finally most frequent, successor to oak.

Table 14. Transition of oaken plots to five classes presented for twenty-year periods by matrix multiplication of decadal observations. Probabilities as percentages. Medium moist sites.

Period	Maple	Oak	Birch	Other	Minor
1927-37	24	50	15	1	10
1937-57	29	42	13	2	14
1957-67	41	6	20	5	28
1967-77	21	7	38	2	32

On moist sites only maple and minor species were most numerous on many of the 56 plots. The only consistent difference was slightly more persistence of minor species on medium moist than on moist sites.

On dry sites only oak was most numerous on many of the 46 plots. The persistence of oak was always greater on dry than on medium moist sites, and after 1937 transitions from oak to maple were always more numerous on dry than on medium moist sites.

On the 42 medium moist sites that were burned in 1932 the transitions of 1927-32 were largely to maple and oak. During the next 25 years minor species became most numerous on many plots. During the final two decades, minor species continued most numerous on more than a third of the plots, while maple became most numerous on a quarter.

The numerous plots on unburned medium moist sites are now examined in another fashion: What steady state are they tending toward? On the left of Fig. 14 are shown the percentages of the 250 plots where each class was most numerous in each year of observation. Minor species held sway on a quarter to a third of the plots. Birch increased its domain to a fifth by 1977 and maple to 36 percent. Meanwhile, oak had fallen from a quarter to less than a fiftieth of the plots.

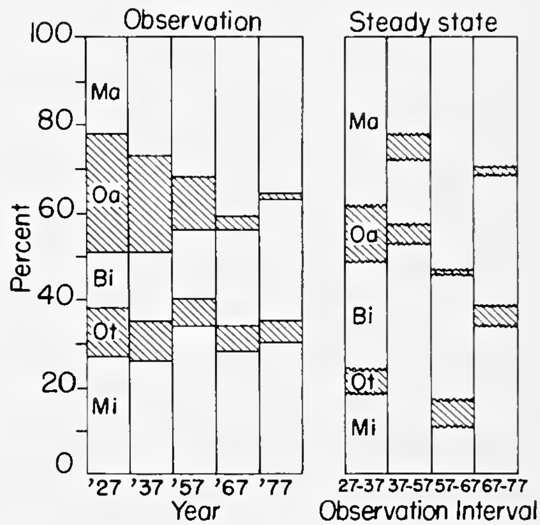

Fig. 14. Left: the change in the kinds of trees most numerous on fortieth-acre plots. Medium moist sites. The heights of the blocks represent the percentage of plots having a class most numerous. Row Ma represents maple; Oa, oak; Bi, birch; Ot, other major species; Mi, minor species. Right: the steady states extrapolated from the four intervals of observation.

The steady states are shown on the right of Fig. 14. Because the transition probabilities varied during the half century, the steady states extrapolated from each period differ. Nevertheless, the results of all periods predict the same general character of the future forest: few plots with oak most numerous and many plots with maple, birch or minor species most numerous. Clearly the decrease in oak and persistence of minor species were not caused by the drought and defoliation

of 1957-67 alone; the trend was underway from the beginning.

Basal area, instead of population, is next used to classify the fortieth-acre plots. Previously a plot of many witch-hazel stems and a large oak would have been classified as "minor species", but now it would be classified as "oak" in calculating the transition probabilities of Table 15.

Table 15. Ten-year transitions in classes of species according to basal area. "Other" means greatest basal area of major species other than maple, oak and birch. Probabilities as percentages. Medium moist sites.

Observed 1937 ↓	Maple	Oak	1927 Birch	Other	Minor
Maple	76	1	0	0	4
Oak	6	96	11	10	23
Birch	18	2	87	8	0
Other	0	1	2	79	5
Minor	0	0	0	3	68
Observed 1977 ↓			1967		
Maple	80	3	4	12	0
Oak	3	90	4	6	0
Birch	11	4	89	13	25
Other	6	2	3	69	25
Minor	0	1	0	0	50

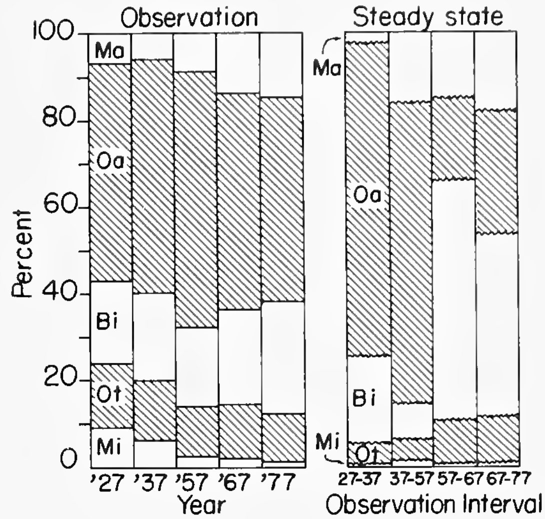

Fig. 15. Left: the change in the kinds of trees with most basal area on fortieth-acre plots. Medium moist sites. The heights of the blocks represent the percentage of plots having a class with most basal area. Row Ma represents maple; Oa, oak; Bi, birch; Ot, other major species; Mi, minor species. Right: the steady states extrapolated from the four intervals of observation.

The striking effect of changing from a criterion of stem numbers to one of basal area is, of course, the lesser persistence of the minor species class and the greater persistence of major species classes, especially oak (Fig. 15). The reader has already seen the decline of the basal area of minor species and the increase of the basal area of major species, and Table 15 is no surprise to him.

Where fire passed in 1932 oak and birch had the greatest basal area on fully three-quarters of the plots in both 1927 and 1967. The persistence of the few maple classifications and the changes in other classifications, however, indicates that the burned tracts will follow the same trend in the future as the unburned.

The change in the transition probabilities on unburned plots from 1927-37 to 1967-77 with the criterion of basal area is smaller than with the criterion of population. Nevertheless, oak persisted less in 1967-77 than in 1927-37. The consequences can be seen in the steady states extrapolated from a declining role for oak, a decline foreseen by Olson (1965) from other evidence; he wrote that the lack of oak recruits "indicate(d) a ... trend toward greater diversity of species in the canopy as opposed to the (1927-57) trend toward increased oak." The initial predominance of oak, a prolific sprouter, was likely a heritage of both fire and repeated clear-cutting for fuelwood and charcoal production, which occurred over much of Connecticut for more than 100 years and the dramatic loss of chestnut from the canopy after 1907. The trend away from oak that has long been indicated by both the lack of recruits and the classification for species according to stem number, and since 1957 the trend in classification according to basal area, has continued after drought and defoliation have

passed. There will likely be a race of the established maple and birch; oak seedlings that appeared on the plots failed to enter the race.

Tolerance

The classification of the plots according to maple, oak and so forth tells much to the viewer of the landscape, but the role of a kind of tree in succession might more logically be appraised in terms of its tolerance of shade, and we turn to that now.

Braun (1950) has succinctly related tolerance and succession:

> "Observations will reveal that young individuals of certain species of trees are commonly seen only in the open while others are seen within the shade of the forests, that some are intolerant, others tolerant. [Tolerance is the ability to develop and grow in the shade of, and in competition with, other trees.] Ecologically, tolerance is of great importance for differences in relative tolerance of species <u>in part</u> determine the progress of succession. Pioneers are generally intolerant species, and often are incapable of growing in their own shade.... Some less intolerant species will grow beneath them, and in time will replace the earlier growth. More and more tolerant trees appear with the progress of succession until finally, in climax communities, the canopy species are ones which can successfully reproduce and maintain ... the community."

Braun goes on to say that, of course, the tolerance of a species may vary from region to region. Nevertheless, the transition from intolerant to tolerant is generally expected as succession proceeds.

The transition among the following four classes on the plots have been examined: very intolerant and intolerant (one class, IT), moderately tolerant (MT), tolerant (T), and very tolerant (VT). The classification of each species is shown in Table 16 and was taken from Baker (1950) or Fowells (1965). Each of the 250 plots employed before was classified into whichever tolerance category had the most stems.

The trend in the tolerance of the species is seen in the transition probabilities (Table 17). A feature of the probabilities is nearer constancy of the transition probabilities for tolerance, Table 17, than for species, Tables 13 and 15. That is, it is reasonable to ask if the transitions in tolerance over the full half century could have been anticipated by multiplying the 1927-37 matrix by itself. The numbers of plots in each class in 1977 and the number predicted were:

	Very Tolerant	Tolerant	Intolerant & Moderately Tolerant
Observed	40	43	167
Predicted	29	42	179

The intolerant and moderately tolerant were pooled because the predicted number of intolerant was less than one. A Chi-square test did not show a significant difference between predicted and observed, evidence that succession among tolerance classes behaves like a simple Markov chain with constant probabilities. Since the forest was a thicket in 1927-37 and since it suffered from drought and defoliation during 1957-67, the constancy of the probabilities is remarkable.

A second feature of the transitions of Table 17 is large probabilities for change to moderately tolerant from the other three classes. (In 1967 there were few intolerant plots, and hence, the probabilities for that column in 1967 in Table 17 are not reliable.) Hence the steady state is predicted to have about two-thirds moderately tolerant plots (Fig. 16). In the plots on moist or dry sites a similar process led to many moderately tolerant or tolerant plots in the steady state. Although some plots will be dominated by both tolerant and very

Table 16. Tolerance to shade (Baker 1950, Fowells 1965). VI indicates very intolerant.

Intolerant (IT)	Moderately Tolerant (MT)	Tolerant (T)	Very Tolerant (VT)
Redcedar (VI)	White Pine	Red Maple	Hemlock
Bitternut Hickory	Shagbark Hickory	Basswood	Sugar Maple
Mockernut Hickory	Red Oak	Shadbush	Beech
Pignut Hickory	Black Oak		Dogwood
Scarlet Oak	White Oak		Bluebeech
Paper Birch	Chestnut Oak		Hophornbeam
Tulip	Yellow Birch		
Bigtooth Aspen (VI)	Black Birch		
Quaking Aspen (VI)	White Ash		
Pepperidge	Black Ash		
Locust	Elm		
Butternut	Chestnut		
Black Cherry	Witchhazel		
Sassafras			
Gray Birch (VI)			

Table 17. Ten-year transitions in tolerance classes according to number of stems. The species in each class are listed in Table 16. Probabilities as percentages. Medium moist sites.

		1927		
Observed 1937↓	Very	Tolerant	Moderately	Intolerant
Very	82	0	2	24
Tolerant	0	79	6	6
Moderately	18	21	92	47
Intolerant	0	0	0	23
Observed 1977↓		1967		
Very	78	0	6	0
Tolerant	8	66	9	0
Moderately	14	32	83	100
Intolerant	0	2	2	0

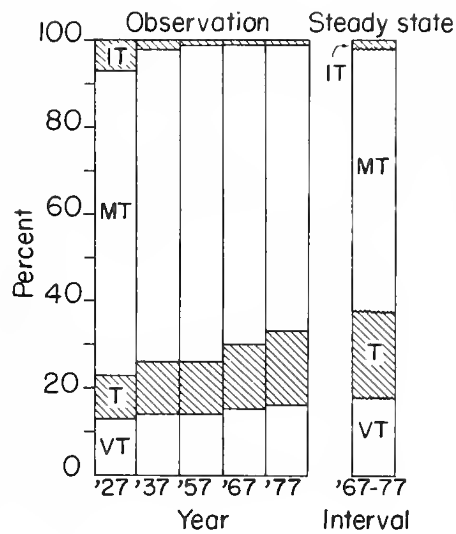

Fig. 16. The change in the tolerance classes with most stems on fortieth-acre plots. Medium moist sites. Left: The heights of the blocks represent the percentage of the plots having a class with most stems. Row IT represents intolerant; MT, moderately tolerant; T, tolerant; VT, very tolerant. Right: the steady state extrapolated from the 1967-77 observations.

tolerant classes, no evidence has been found of a large trend on to the very tolerant class.

Thus both phenomena mentioned by Braun (1950) are visible in the Connecticut forests. First, the succession away from intolerant is clear. But the superficial expectation that succession would go on to very tolerant has been confounded by the regional bounds of species. The very tolerant hemlock, sugar maple, and beech have so far been unable to prevail in Central Connecticut. The long life of many moderately tolerant species undoubtedly contributes to the persistence of that class. Hence the four forests needed to lose only a few intolerant trees to reach essential equilibrium, midway in the classes of shade tolerance.

The speed of succession can be learned by simulating succession with the probabilities of Table 17. This is reasonable because they have proven similar

from decade to decade, and we shall use the precise values for 1927-37.

Fig. 17 shows the simulated succession following an invasion and complete domination of an old field by pioneering intolerant species. The first column, the initial state, is wholly plots dominated by intolerant. The intolerant gray birch died in the real field near Cabin in 1920 (front cover). On the hillside in front of the cabin is land dominated by gray birch as in the initial state of our simulated succession, left column of Fig. 17.

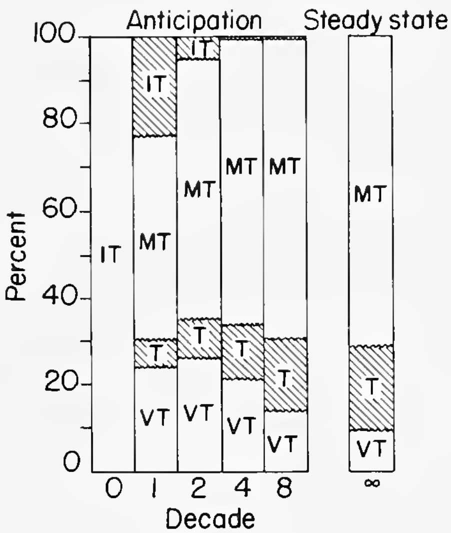

Fig. 17. Simulated succession of tolerance classes upon an old field. Left: the heights of the blocks represent the proportion of fortieth-acre plots dominated by the stem population of a tolerance class. In the initial state, 0, represented by the leftmost column all plots in the old field are dominated by the intolerant (IT) class. The columns to the right show the appearance of dominance by moderately tolerant (MT), tolerant (T) and very tolerant (VT) species after 1, 2, 4 and 8 decades as calculated from the 1927-37 transition probabilities, medium moist sites. Right: the rightmost column shows the anticipated steady state.

At the end of the first decade, which is depicted by the second column, the pioneering intolerant species have lost three-quarters of their territory and rule over only a quarter of their former kingdom. The moderately tolerant already dominate nearly half the field. The tolerant and very tolerant have already appeared. By the end of the fourth decade the moderately tolerant dominate two-thirds and the pioneering intolerant have practically disappeared. Only small changes occur thereafter until the field has reached the steady state depicted by the column at the right of Fig. 17.

The reader may doubt the rapidity of this synthetic succession, especially when confronted by Bard's (1952) well-known estimate that 100 years would be required for oaks and hickories to dominate succession in the New Jersey Piedmont. However, Bard was considering the time required to change from grassy field to hardwood forest. In our example we assumed the tract occupied by intolerant trees. Further, Bard's tract contained no gray birch but was dominated by redcedar. Lutz (1928) said,

> "...the higher the percentage of gray birch in the redcedar-gray birch association, the faster the succession will move. Gray birch stands usually deteriorate between thirty to sixty years old. On better sites redcedar is usually over-topped and dies when it is sixty to eighty years old."

In 1927 our tracts contained many gray birch but few redcedar (Table 2), and the transition probabilities were derived from plots with trees, not grassy fields. Hence, the relatively short time required for intolerant hardwoods to disappear seems reasonable.

Because the simulated succession appears to progress reasonably one might ask how long would be required for our real forest to attain their predicted steady state. In theory attainment of steady state may require infinite time. Since, however, classification of our forest plots is not a precise endeavor, an approximation may suit our purposes. Accordingly, the transpose of the matrix of observed transition probabilities was premultiplied by the vector containing the number of plots in each class. The resultant vector, containing the redistribution of plots after one interval of transition, was compared with the estimated distribution at steady state. The

multiplication was repeated until all classes were within a specified percentage of the predicted steady state. When the steady state was approximated the time required was estimated by the product of the number of multiplications necessary and the interval of transition.

For example, when the 250 medium moist plots were classified into species groups according to number of stems we see the predicted steady states (Fig. 14). From the 1927-37 transitions we predicted 39 percent maple, 13 oak, 25 birch, 6 other major and 18 percent minor species. The time required to come within 1 percent of each of these values was 170 years. Extrapolating from the 1967-77 transitions we estimate 70 years to approximate the steady state. Both values from observations 40 years apart appear realistic. They indicate attainment of the steady state or climax within an attainable life span for the trees and forest. Thus our confidence in the transitions is increased.

Turning to other criteria such as basal area or tolerance to shade we again attain reasonable estimates but only with some relaxation of our stringent requirement for approximation. For example, when basal area is the basis for classification into species groups we attain approximation of steady state by the 1927-37 transitions at 200 years and by the 1967-77 at 190 years when the approximation was relaxed to 5 percent. When we base our classification on shade tolerance according to number of stems we estimate a very long time to approximate within 2 percent the steady state predicted by the 1927-37 transitions but only 50 years when employing the transitions of 1967-77.

Since much the same course of succession is anticipated from the transition probabilities of all decades it seems reliable. Some anecdotes, although less sound than the transition probabilities themselves, help persuade one of the realism of the simulated succession. In 1927 crowds of gray birch grew on the Cox tract, and 40 years later few remnants could be found. In 1927 intolerant species were predominant on 17 medium moist plots. In 1937, this class retained control of four; in 1957, two; in 1967, three; in 1977, only four. Finally the photographs on the front and rear covers show that the pioneering, intolerant gray birch had been eliminated long before by its more tolerant competitors. And the large tree in the foreground is a red maple, which belongs to the tolerant class that the synthetic succession of Fig. 17 makes prominent in the steady state forest.

Diversity

The viewer who likes variety in his landscape as well as a man who wants insurance against forest destruction by a single pest is interested in other changes in the quality of the forest, and the foregoing classes will not serve. Rather, the viewer and the insurer want to anticipate whether the forest will become more or less diverse. The diversity index (Pielou, 1966), which was introduced earlier in this Bulletin, is a criterion that indicates an increasing number of stems and species and a broader distribution of stems among species. It was, therefore, calculated for the 250 chain lengths of transect, and the transition probabilities are tabulated in

Table 18. Ten-year transitions in diversity per plot. The diversity classes are: Low, less than 1.80; B, 1.80 to 2.09; C, 2.10 to 2.40; High, greater than 2.40. Probabilities as percentages. Medium moist sites.

Observed 1937 ↓	1927 Low	B	C	High
Low	79	47	10	6
B	18	45	46	10
C	3	6	41	49
High	0	2	3	35
Observed 1977 ↓	**1967**			
Low	77	35	0	0[a]
B	17	46	53	50[a]
C	6	19	41	0[a]
High	0	0	6	50[a]

[a] Sample of 2.

Table 18.

The probabilities are much the same for the first and last decades: a transition to lower diversity. This was also evident in the dry decade of 1957-67. Since the number of stems per fortieth-acre plot decreased, it is not surprising that diversity has also decreased. Thus although the diversity of the forest on the entire 10.12 acres of transect scarcely changed as noted in an earlier section, the diversity of trees on the fortieth-acre plots surely declined, and the trend is for a further decrease to a steady state of half to two-thirds of the plots in the lowest class of 1.80 to 2.09 and few in the more diverse classes.

FUTURE

After a half century of observation, what can be extrapolated to the future?

The forest represented by our tracts is mature. That is, the stems of major species have now stabilized at about 500 per acre, increasing some when a pest makes openings and likely decreasing again. The basal area of the stems has also stabilized at about 100 ft^2 per acre. Dry sites have a larger population and a smaller basal area, but the differences are small and seem destined to remain surprisingly small.

Fire removes saplings and thus encourages ingrowth, but after a few decades its effect is slight. Defoliation and drought have scarcely detectable effects after a decade or two.

With the pioneer species long dead and the minor species remaining minor, the future forest seems certain to be dominated by a few major species. The diversity of the entire forest will likely continue great, but the diversity of small tracts will surely be less. The steady states predicted from transition probabilities have populations dominated by maple, birch and minor species, but the basal area seems destined to be dominated by maple, birch and oak. New maples and birches appear but only slowly grow large enough to contribute much basal area and the large oaks are only slowly removed by death.

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State Foresters H. A. McKusick, E. J. Vandermillen and R. L. Garrepy have vigilantly protected these tracts whose historical and scientific value has increased many-fold since their inception in 1926-27.

In 1972, through the efforts of the late H. A. McKusick and the Natural Area Preserves Advisory Committee, these tracts became the first tracts of the Connecticut Natural Area Preserve System.

COMMON AND SCIENTIFIC NAMES OF PLANTS MENTIONED IN THIS BULLETIN

Ash, white -- *Fraxinus americana*
   black -- *F. nigra*
Aspen, bigtooth -- *Populus grandidentata*
   quaking -- *P. tremuloides*
Basswood -- *Tilia americana*
Beech -- *Fagus grandifolia*
Birch, black[1] -- *Betula lenta*
   yellow -- *B. alleghaniensis*
   paper -- *B. papyrifera*
   gray -- *B. populifolia*
Bluebeech[1] -- *Carpinus caroliniana*
Butternut -- *Juglans cinerea*
Cherry, black -- *Prunus serotina*
Chestnut, American -- *Castanea dentata*
Dogwood, flowering -- *Cornus florida*
Elm, American -- *Ulmus americana*
Hemlock -- *Tsuga canadensis*
Hickory, bitternut -- *Carya cordiformis*
   shagbark -- *C. ovata*
Hickory, mockernut -- *C. tomentosa*
   pignut -- *C. glabra*
Hophornbeam -- *Ostrya virginiana*
Locust, black -- *Robinia pseudoacacia*
Maple, sugar -- *Acer saccharum*
   red -- *A. rubrum*
Oak, white -- *Quercus alba*
   chestnut -- *Q. prinus*
   red -- *Q. rubra*
   scarlet -- *Q. coccinea*
   black -- *Q. velutina*
Pepperidge -- *Nyssa sylvatica*
Pine, white -- *Pinus strobus*
Redcedar[1] -- *Juniperus virginiana*
Sassafras -- *Sassafras albidum*
Shadbush[1] -- *Amelanchier arborea*
Tulip[1] -- *Liriodendron tulipifera*
Witchhazel -- *Hamamelis virginiana*

[1] Local name differing from Little (1953) or Standardized Plant Names (Kelsey and Dayton, 1942).

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Rear Cover: By 1966 when this picture was taken, the open field and birches shown on the front cover had long since passed from view in this unmanaged area.